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SYNOPSIS OF BIOLOGICAL DATA ON SMELT
Osmerus eperlanus (Linnaeus) 1758

Prepared by
T. N. Belyanina

FAO
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no. 78

FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
ROME, 1969

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SAST Datos relativos a ciertas especies y poblaciones.

MAST Sinopsis sobre métodos y materias.

OT Sinopsis sobre oceanografía.

IT Sinopsis sobre limnología.

y

CART Información sobre los recursos acuáticos vivos de algunos países y regiones (FID/S).

Grupos especiales de documentos técnicos se identifican por las siglas siguientes:

RE Listas índices de expertos y de instituciones tomadas de los registros que se llevan en la Dirección de Recursos Pesqueros y Explotación.

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FAO Fisheries Synopsis No.78
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SAST - Smelt - 1,23(04),003,01

SYNOPSIS OF BIOLOGICAL DATA ON SMELT

Osmerus eperlanus (Linnaeus) 1758

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, December 1969

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PREPARATION OF THIS SYNOPSIS

The preparation of this Synopsis was promoted in view of the need to review the abundant and much scattered information on the biology and exploitation of Osmerus eperlanus which is the main object of a number of fisheries in the northern hemisphere.

The details set out in this paper are based on data collected by the author in the course of personal research work on the species and also, on information received from various sources, most of which are listed in the Bibliography.

The author and the editor are grateful to Dr. D.I. Williamson, Marine Biological Station, Port Erin, Isle of Man, U.K., for his editorial work on the synopsis.

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1. IDENTITY

1.1 Nomenclature

1.11 Valid name

Osmerus eperlanus (Linnaeus, 1758).
Original combination: Salmo Eperlanus Linnaeus, 1758, Syst. Nat. (ed. 10), p. 310

1.12 Objective synonymy

Salmo eperlano-marinus Bloch, 1782, Naturgesch. d. Fische Deutschlands 1, p. 128, Pl.28, Fig.1.

Osmerus eperlanus: Lacépède, 1804, Hist. nat.des Poissons, 5, p. 229.

Salmo (Osmerus) eperlanus: Pallas, 1814, Zoogr.Ross.As., 3, p. 386.

1.2 Taxonomy*

1.21 Affinities

Suprageneric

Superphylum-Chordata
Phylum-Vertebrata
Subphylum-Craniata
Superclass-Gnathostomata
Series-Pisces
Class-Teleostomi
Subclass-Actinopterygii
Order-Clupeiformes
Suborder-Salmonoidei
Family-Osmeridae
Subfamily-Osmerinae

Generic

Osmerus Linnaeus, 1758, Syst.Nat. (ed. 10) p. 310. Type species: Salmo eperlanus Linnaeus, 1758. /Linnaeus (1758) adopted four sub-divisions of his genus Salmo, one of which he named 'Osmeri'. The generic name Osmerus Linnaeus, 1758, with type-species Salmo eperlanus Linnaeus, was validated in Direction 69 of the International Commission on Zoological Nomenclature./
"One large canine on either side of vomer, sometimes accompanied by smaller ones. Palatine teeth enlarged anteriorly. Maxillary extends to about posterior border of orbit. No striae on opercle or subopercle. Distance from snout to dorsal origin shorter than from dorsal origin to caudal base. A midlateral ridge, but no anal shelf or elongated midlateral scales in male. Gill-rakers 25 to 37. Pyloric caeca 3 to 8. Stomach with blind sac. Lower jaw spatulate. Anal rays 11 to 14. Midlateral scales 58 to 72. Lateral line incomplete. Adipose base about two-thirds of orbit diameter (rarely in large specimens equal to orbit). Orbit diameter two-thirds or less of caudal peduncle depth. Proethmoids double. Mesethmoid simple, without other ossifications. Parietals completely separated by supraoccipital. Pterosphenoids not reaching parasphenoid anteriorly. Slit present between hyomandibular. Four simple actinosts". (McAllister, 1963).

Anadromous or landlocked forms in the Polar, Pacific and Atlantic Oceans and their drainages.

Subjective generic synonyms

Eperlanus Gaimard, 1850-52, Voy. en Islande et Groenland, Paris. Atlas, pl.XVIII, fig.2 (type-species: Eperlanus vulgaris Gaimard).

Allosmerus Hubbs, 1925, Proc.Biol.Soc.Wash., 38, p. 53. (type-species: Osmerus attenuatus Hubbs).

Specific

Three forms of the boreal smelt have generally been recognized; O. eperlanus of the North and Baltic seas, O. dentex of the Pacific north into the Arctic and west to the White Sea, O. mordax of the Western Atlantic. Following detailed studies of their populations Berg (1948), Andriashev (1954) and other Russian workers have reduced dentex to a subspecies of eperlanus. Some american authors (Kendall, 1927; McKenzie, 1958, and others) consider the american smelt as a separate species, but Bigelow et al. (1963) and McAllister (1963), who made a revision of the Osmeridae, considered that the genus Osmerus includes only one species, O. eperlanus (L).

1.22 Taxonomic status

It is a morpho-species, a polytypic species with many geographical and ecological forms.

1.23 Subspecies

Key to subspecies of Osmerus eperlanus (from McAllister, 1963).

1(2) Pored scales in the lateral line usually 14-28 (rarely 13-30). Western Atlantic, Pacific and Arctic west to the White Sea and their drainages ..... Osmerus eperlanus mordax (Mitchill)

*After Berg (1948) and McAllister (1963)

2(1) Pored scales in the lateral line usually 6-13 (rarely 0-16). Baltic and North seas and their drainages and Upper Volga River ..... Osmerus eperlanus eperlanus (Linnaeus)

Osmerus eperlanus mordax (Mitchill) 1814*

Atherina mordax Mitchill, 1814, p. 15, New York (Speirs 1951, indicated that this was the type description).

Osmerus viridescens Le Sueur, 1818, p. 230, coast of Maine.

Osmerus sergeanti Norris, 1868, p. 93, Schuylkill River, New Jersey (described but not named by Norris, 1868, p. 58).

(Osmerus sergenti auctorum).

Osmerus spectrum Cope 1870, p. 490, Wilton Pond, Kennebec County, Maine.

Osmerus dentex Steindachner, 1870, p. 429, Dekastris Bay, USSR.

Osmerus dvinensis Smitt, 1882, p. 32, Northern Dvina River, Russia.

/The following natios named by Petrov, 1925 p. 82, 108, have no status under the rules of the Int.Comm.Zool.Nomencl: Osmerus e. dentex natio kaninensis, Cheshskaya Gulf; O.e. dentex natio jenisseensis, Enisey River at Tyurin and some other localities/.

Diagnosis

Distinguished from other osmerid species by the two large canines, one on either side of the vomer opercular striae; the maxillary extending past the pupil. 4 to 8 pyloric caeca. This subspecies is distinguished from O.e. eperlanus by the greater number of pored lateral line scales, usually 14 to 28.

Description

D 8-10(11); C 19; A (12)13-15(16); V 8; P 11-13(14); LL (13,14)15-28(29,30); midlateral scales (62)63-69(72); vertebrae (58,59) 60-66(67,68,70); gill-rakers 8-11 + 18-24 = (26) 27-36(37); branchiostegals (6)7-8; pyloric caeca 4-8. Standard length 3.8 to 4.4 times head length, 4.7 to 7.4 times depth. Pectorals reaching from one-half to two-thirds the distance to pelvic insertion; pelvic a little more than half way to anal origin. Adipose base short, about two-thirds of eye diameter.

Medium sized canines on dentary, enlarging posteriorly. Small pointed teeth on premaxillary and maxillary. Canines on anterior end of tongue enlarged. Pelvic origin anterior to dorsal origin. Ductus pneumaticus attached to anterior end of gas bladder. Lateral line incomplete, ceasing about a head's length along the body.

Peritoneum light with dark speckles, more intense dorsally. Ventral portion of body pale; dorsum speckled with black, more intensely around exposed borders of scales. Chin and top of head evenly speckled. A dark mediolateral bar without sharply delimited border. In life sides an iridescent silver, the back an olive green. Total length to 324 mm according to Berg (1948). A larger subspecies than O.e. eperlanus.

Osmerus eperlanus eperlanus (Linnaeus) (Fig. 1).

Salmo eperlanus Linnaeus, 1758, p. 310. European seas and rivers.

Eperlanus Schonfoldii Rutty, 1772, p. 358, Ireland.

Salmo eperlano-marinus Bloch, 1782, p. 229, Table 28, Fig. 1, northern and Baltic seas and into rivers.

Salmo eperlanus var. marinus Walbaum, 1792, p. 57.

Salmo spirinchus Pallas, 1814, p. 387, lakes and rivers. Germany, European Russia, (Beloozero, Chudsk, and other localities).

/Eperlanus Rondeletii Willughby, 1789, p. 202, Table 6, Fig. 4, Anadromous in Thames (unavailable since it is a reprint of a pre-Linnaean edition originally published in 1686)/.

Salmo eperlanus marinus: Walbaum, 1792, p. 57 (ex. Bloch).

/Eperlanus fluviatilis Gesner, in the synonymy for Salmo eperlanus of Donovan, 1804, p. 189 (not available, a pre-Linnaean name cited in a synonymy)/.

Eperlanus vulgaris Gaimard, 1851, p. 207, p. 18, Fig. 2, Iceland (this species not known in Iceland before or since this time according to Saemundsson, 1949).

Osmerus e. eperlanus natio ladogensis Berg, 1932, p. 281, Lake Ladoga (infrasubspecific names have no status under the Int.Rules Zool.Nomencl.)/

* Diagnosis, description of subspecies and synonymy by McAllister (1963:15-21).

Diagnosis

This subspecies is distinguished from O.e. mordax by the lower number of pored lateral line scales, 4 to 13.

Description:

D 7-9; C 19; A (11)12-13 (14); V 8; P 11-12(13); LL (0)4-13(16); midlateral scales (58)61-69; vertebrae (55,56)57-61(62,63); gill-rakers 25-37; branchiostegals 7(8), pyloric caeca 3-7. Standard length about 4 to 5 times head length, 5.6 to 6.1 times depth; pectorals extend one-half to two-thirds the distance to the pelvic insertion; pelvics about half-way to anal origin. Adipose base short, about two-thirds the orbit diameter.

Medium sized canines on dentary, enlarging posteriorly. Small pointed teeth on premaxillary and maxillary. Ductus pneumaticus attached to anterior end of the air bladder. Lateral line incomplete, ceasing less than a head's length along the body.

Peritoneum light with dark speckles. Back greenish, sides silver in life. Total length to 307 mm according to Berg (1948). A smaller form than O.e. mordax.

1.24 Standard common names and vernacular names - See Table I.

TABLE I
Standard common names and vernacular names of Osmerus eperlanus (L.)

Country	Standard common name	Vernacular name
England	smelt	
France	éperlan	
Netherlands	smaelt	
Finland	kuore	
Sweden	nors	
Norway	nors	
Canada	smelt, éperlan	
USA	smelt	rainbow smelt
USSR	koriushka	zubatka, ogurechnik, koreha, snetok, tint, norss, salaka.
Japan	kyuri-uwo	

1.3 Morphology

1.31 External morphology

McAllister (1963), who studied the geographical variability of smelt, came to the conclusion that the only difference between dentex and mordax is the vertebral number (Table II), however this may be because of lower water temperature during the development of dentex eggs. McAllister therefore considered dentex a synonym of mordax. Mordax and eperlanus differ considerably (especially number of pored lateral line scales - Table VI). Using this character alone over 90 percent of all the specimens of both forms can be separated. Since the two forms are allopatric and since vertebral and anal ray differences all overlap considerably it is necessary to consider the two forms as subspecifically different. The difference is nonclinal (McAllister, 1963).

Data on plastic characters of different smelt populations of Europe and Asia are given in Tables III-V, on meristic characters in Table VI.

Plastic characters of the smelt vary considerably with age (especially height of fins and their situations, width of forehead, eye diameter). Kirpichnikov (1935) found that height of fins decreases with growth: correlation coefficients between height of A and standard length (L) in the White Sea smelt were -0.40 and - 0.45 (for various samples), between height of D and L were -0.38, -0.42, -0.73; between P and L were -0.45 and -0.47, between V and L -0.54. Eye diameter also shows a negative correlation: -0.79 and -0.75. Snout length and forehead width increase with age: the correlation coefficients were + 0.66 and +0.75. Values of A-V, P-V, D-d also increase, although the correlation coefficient is rather low (usually less than +0.50).

The smelt scale is very specific (Figs. 2, 3). "The smaller year-old smelt has scales with relatively large focus and no complete circuli in the first growth field whereas scales of the larger fish have a smaller focus and one to several completed circuli. Both types however exhibit clearly the diagnostic features of a gradual shortening of the horseshoe-shaped incomplete circuli as growth slows in late season and a distinct cutting over the first circulus of the second growing season. Later annuli are easily recognizable. A growth field contains a series of complete circuli that gradually shorten as growth slows. The first circulus that appears in the following growing season cuts across these shortened circuli" (Bayley, 1964). The year annuli form as scars outside the series of incomplete circuli of the last growing season (Figs. 2, 3). Annulus formation starts near June. Circulus number in the successive years of growth in different smelt populations is shown in Table VII.

Fig. 1 Osmerus eperlanus eperlanus (L) (from Berg, 1948)

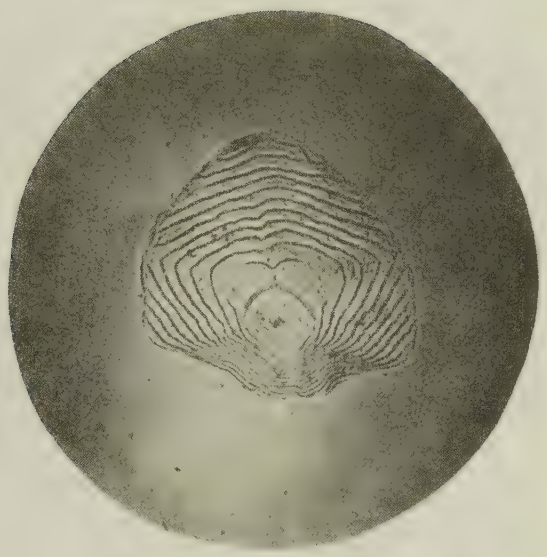


Fig. 2 Scale of 2 year-old smelt. White Sea. Magnif. 6 x 3.

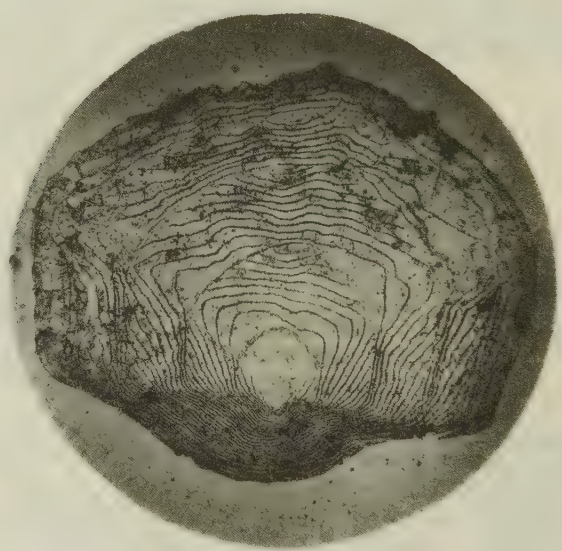


Fig. 3 Scale of 5 year-old smelt. White Sea. Magnif. 6 x 3.

TABLE II

Comparison of different forms
of Osmerus (McAllister, 1963)

Characters	Dentex	Mordax	Eperlanus
L.L. (min.-max.)	15-28 (13-30)	14-19 (13-19)	6-13 (0-16)
vertebrae (min.-max.)	63-66 (59-70)	60-63 (58-65)	58-61 (55-63)
Head L/anal height	2.6-3.2	2.3-4.4	2.3-2.6
Modal anal rays	13-14	13-15	12-13
Dorsal rays	8-10	9-10	7-9
Pectoral rays	12-13	(11)12-13	11-12(13)
Midlateral scales	63-72	63-65	61-69
Gill rakers	26-35	28-35	25-37
Pyloric caeca	5-8	4-7	3-7

TABLE III

Data on fins (as % of body length)*
(after Kirpichnikov, 1935; Nikolsky, 1956, and others)

Locality	Height of D	Height of A	Height of P	Height of V	Length of D base	Length of A base
White Sea	12.7-16.7	7.0-9.8	14.8-15.3	12.4-12.9	8.2-8.6	11.9-12.9
Chesha Bay	14.9-16.7	8.4	15.3	13.0	8.0-9.2	12.3-13.2
Pechora River	16.1-17.0	10.8	-	-	7.8-8.3	13.3
Pskov-Lake	16.3	9.8	-	-	8.5	12.4
White Lake	16.7	10.7	-	-	8.6	13.2
Finnish Gulf	15.0	9.5	-	-	8.7	12.9
Onega-Lake	16.9	10.3	15.2	13.8	8.2	13.2
Ladoga-Lake	12.4-14.5	9.3-10.3	14.6	13.1	7.7	14.3
Neva River	15.7	9.9	15.1	13.6	8.7	12.3
Far East	12.2-14.9	6.9-8.0	14.1-15.6	12.3-13.9	7.5-8.3	10.9-12.9
Yenisey River	12.8-13.7	7.3-8.4	14.9-15.3	13.0-13.2	8.6	12.8
Norway	14.3	9.2	14.7	13.3	8.1	12.4

*These are averages of different samples, not min.-max. values of characters.

TABLE IV

Data on head* (after Kirpichnikov, 1935; Nikolsky, 1956, and others)

Locality	Head length (as % of standard length)	Snout length (as % of standard length)	Eye diameter (as % of head length)	Forehead width (as % of head length)	Lower jaw (as % of standard length)	Upper jaw (as % of standard length)
White Sea	21.2–23.8	5.7–7.0	16.6–20.9	20.4–24.8	12.5–14.3	7.6–9.6
Chesha Bay	21.7–22.4	6.0–6.9	21.1	20.4	13.1–13.8	8.9–9.3
Pechora River	19.9–21.3	4.9–5.6	19.0	–	10.9–11.0	7.8–8.2
Pskov Lake	20.9	4.7	21.2	24.9	11.4	8.3
White Lake	21.0	4.9	21.9	25.3	11.8	8.5
Finnish Gulf	22.5	7.0	27.1	19.1	11.3	9.2
Onega Lake	22.8	–	22.3	24.5	–	–
Ladoga Lake	21.8–22.5	7.2	20.6–24.8	20.5–21.4	13.0	11.2
Neva River	22.3	–	19.6	23.7	–	–
Norway	22.3	–	19.9	25.1	9.8	14.8
Yenisey River	21.6–21.7	6.9	19.0–20.6	22.8–25.3	8.6	13.0
Far East	21.4–21.5	7.1–7.5	19.9–20.6	22.8–25.3	8.6	12.8

*These are averages of different samples, not min.–max. values of characters.

TABLE V

Plastic characters of smelt (as % of standard length)
(after Kirpichnikov, 1935; Nikolsky, 1956, and others)

Locality	Maximum body depth H	Minimum body depth h	A–D	A–V	P–V	V–A	Preanal length	D–d	Caudal peduncle length
White Sea	12.7–16.0	4.8–5.4	45.8–47.8	45.3–49.7	25.1–27.3	21.2–23.4	70.7	18.8–21.7	11.5–13.9
Chesha Bay	13.0–16.2	4.8–5.1	45.7–46.6	46.4–48.5	24.5–27.6	22.1–23.3	–	19.8–21.8	11.0
Pechora River	12.1–16.1	5.1–5.6	45.3–46.9	44.5–46.9	23.5–27.4	24.0–25.5	–	19.6–20.3	12.3
Pskovsko-Chud.l	14.6	5.0	47.2	46.1	25.9	23.7	–	18.5	11.6
White Lake	14.5	5.5	47.4	46.7	24.1	22.9	–	18.0	10.6
Finnish Gulf	15.6	5.4	47.6	47.9	26.4	22.4	–	18.6	12.2
Onega Lake	13.3	5.0	49.9	–	27.4	22.2	–	19.9	11.7
Ladoga Lake	15.6–16.3	4.7–5.0	49.3–49.8	49.1	27.9–28.1	24.2	70.4	19.9	11.3–12.5
Neva River	15.9	5.3	48.6	–	26.6	22.6	–	19.7	12.3
Far East	14.8–16.5	5.2	47.2–47.8	–	26.1–27.1	22.1–22.2	70.2	–	11.6–11.9
Yenisey	14.3–14.4	4.7–5.2	45.8–46.2	46.9–47.7	25.9–28.1	22.7–23.0	68.5–70.3	–	12.1–12.7
Norway	–	5.1	48.8	49.3	27.2	23.0	71.1	–	11.2

TABLE VI

Meristic characters of different smelt populations
(after Kirpichnikov, 1935; Nikolsky, 1956; Lillelund, 1961)

Locality	Gill-rakers	Vertebrae	Pored scales in LL	Rays in D		Rays in A	
				Unbranched	Branched	Unbranched	Branched
White Sea	29-38	60-67	15-27	1-3	5-10	2-4	12-16
Chesha Bay	26-34	62-67	16-24	-	-	-	-
Pechora River	31-35	58-63	7-8	2-3	7-8	3-4	12-14
Pskovso-Chudskoye l	32-35	58-60	-	2	8-9	3	12-14
White Lake	32-37	57-60	-	2-3	7-9	3	11-13
Finnish Gulf	32-36	59-62	8-10	2-3	8-9	3-4	11-13
Onega Lake	30-35	-	-	2-3	8-9	-	-
Ladoga Lake	-	-	4-11	2-3	10-11	3	12-14
Neva River	-	-	4-11	2-3	8-9	-	-
Far East	27-33	66	18-28	2	9	3	12-14
Yenisey River	26-32	66-67	14-26	2-3	9	3	13
Norway	-	59-62	-	-	-	-	-
Baltic Sea	-	59-62	10-13	-	-	-	-
Chukotka	-	-	14-20	-	-	-	-
West Germany	26-33	55-60	4-11	-	-	-	-

TABLE VII

Circulus number in the successive years of growth in different smelt populations

Locality	Years of growth					Authority
	1	2	3	4	5	
Rivers of East England	14	18	9-10			Masterman 1913
Miramichi River (min.-max.)	10 0-19	15 10-20	7-8 4-12			McKenzie 1958
White Sea (min.-max.)	2-3 0-6	9 7-12	9 8-13	5 4-7	4-5	Original

1.32 Cytomorphology (Chromosome number etc.)

Svärdson (1945) found that "the smelt has short and slender chromosomes, considerably smaller than in the other species. Their number is the lowest among the Swedish representatives of the Salmonidae family, their diploid number being merely 58. As a rule, however, both V-shaped and rod-shaped chromosomes occur. There are five pairs V-shaped chromosomes. Two of them arms of approximately equal length whereas other three pairs have one markedly long arm. Constrictions may occur distally in the short arm of one of those chromosome pairs. The rod shaped chromosomes vary in length. Thus the longest rod-shaped pair at any rate in certain early metaphases may be four times as long as the shortest. One of the rod-shaped pairs has proximal constriction. The meiosis was not studied".

Owsiannikov (1885), Cunningham (1886 - cited by Lillelund, 1961) and Lillelund (1961) have described ripe oocytes of the smelt, their membranes and micropyle. Lams (1904) studied vitellogenesis of smelt. Kuznetzov

(1964) gave a comparative analysis of oogenesis of the migrant smelt of the Neva river and non-migrant small-sized smelt (snetok) of the Pskov lake. He found that the oocytes of the Neva river smelt are larger than those of the Pskov lake at the same phases of oogenesis. Oogenesis has also been studied in the White Sea smelt. According to Meyen (1939, 1944) the period of protoplasmatic growth of oocytes includes the juvenile phase and the one-layer follicle phase. During the juvenile phase the oocyte size in the White Sea smelt is about 13.5-36 µ, the nuclear diameter is 11.3-27 µ. The cellular membrane is thin and has no visible structures. The cytoplasm is granular. There are 7-10 nucleoli in the nucleus (in a section). During the one-layer follicle phase the oocyte size is from 45 to 112 µ, the nuclear diameter is from 36 to 76.5 µ. At the periphery of the nucleus there are 20-40 nucleoli. The oocyte is rounded, the cellular membrane is thin. There is a more intensely coloured circumnuclear zone at some distance from the nucleus which disappears after vacuolization has started (Fig. 4).

The period of trophoplasmatic growth of smelt oocytes may be divided into 4 phases. During the phase of marginal vacuolization the oocyte diameter is about 144 µ, the nuclear diameter is about 81 µ. A series of little vacuoles appear at the periphery of the oocyte (Fig. 4); these vacuoles do not contain oil. During the phase of initial accumulation of vitellin and oil the oocyte diameter is 80-160 µ, the nucleus is oval but in section its margin is festooned. At the periphery of the nucleus there are 6-12 nucleoli. The cytoplasm is vacuolated (Fig. 5); the peripheral vacuoles contain oil, the circumnuclear ones contain vitellin. The oocyte membrane is a one-layer zona radiata. During the phase of intensive trophoplasmatic growth (Fig. 6) the oocyte diameter measures from 320 to 550 µ. The oocyte is round or slightly oval. The long nucleus is in the middle. Its margin is heavily festooned. The nuclear diameter is about 100 µ. There are from 4 to 12 nucleoli at the periphery of the nucleus (in a section). The cytoplasm is heavily vacuolated and the vacuoles contain more oil (Fig. 7). Granules of vitellin, previously in the vacuoles, now appear in the cytoplasm. The oocyte membrane is thick and consists of two layers: zona radiata externa and zona radiata interna. The first is more clearly striated (Fig. 6). Both membranes form a little hollow at the formation of the micropyle. During the phase of ripeness the oocyte of the White Sea smelt reaches its definitive size (about 800-900 µ). The nuclear diameter is about 120 µ. The nucleus is oval, its margin is festooned in section. At the beginning of the phase there are 6-12 nucleoli at the nuclear periphery but then

Fig. 4 Smelt oocytes during the juvenile phase (right) and the end of the phase of one-layer follicle. Magnif. 10 x 90. Stain: iron haematox. (Heidenhein)

Fig. 5 Smelt oocytes during the phase of initial accumulation of vitellin and oil. Magnif. 10 x 8. Stain: Mallory

they disappear. Vitellin granules and oil globules of various sizes fill in the oocyte. A very thin layer of fine-grained cytoplasm adjoins the oocyte membrane from within. The oocyte membrane consists of two layers of zona radiata; the thickness of zona radiata externa is about 11.3 µ, the thickness of zona radiata interna is about 13.5 µ. The micropyle is definitively formed (Fig. 8). The animal and the vegetative poles of the egg are defined. The nucleus moves from the middle of the egg towards the micropyle. The layer of fine-grained cytoplasm is thickest at the micropyle (Fig. 8). Vitellin and oil form a homogeneous mass at the vegetative pole. After ovulation eggs come into the body cavity and are then shed. Generally growth and development of oocytes in the White Sea smelt last 3-4 years, the period of protoplasmatic growth being the longest.

1.33 Portein specificity

Studies on this question are not yet published, but Rupp and collaborators are working on it (Rupp and Redmond, 1966).

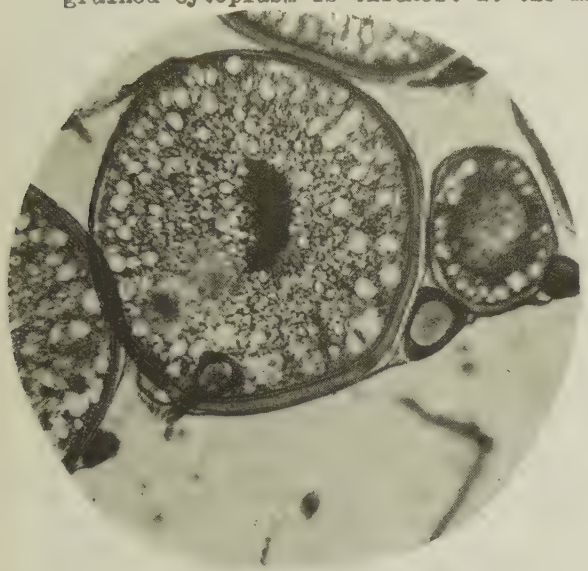


Fig. 6 Oocytes in the phase of intensive trophoplasmatic growth. Magnif. 10 x 40. Stain: Mallory

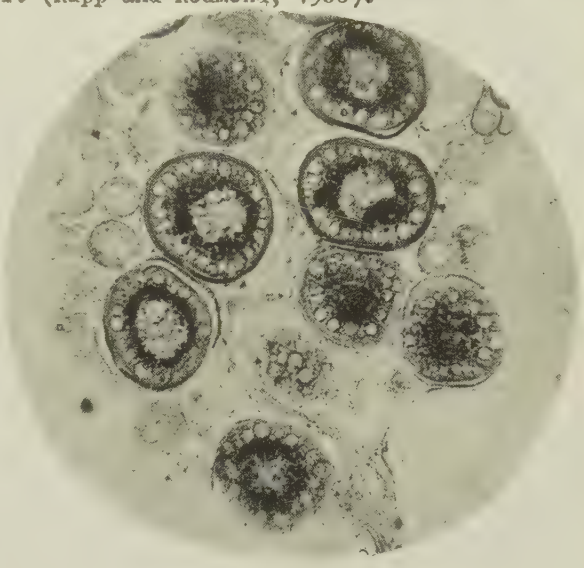


Fig. 7 Oocytes in the phase of intensive trophoplasmatic growth. Magnif. 10 x 8. Stain: Sudan-III

Fig. 8 Part of an oocyte in the phase of ripeness. Magnif. 10 x 20. Stain: Mallory

2. DISTRIBUTION

2.1 Total area

Anadromous and landlocked fishes in the Pacific, Arctic and Atlantic oceans and their basins (Fig. 9). According to McAllister (1963), "the simplest explanation of the unusual distribution of the two subspecies (particularly the Arctic hiatus of O. eperlanus mordax) involves an origin of the species in the North Pacific or adjacent Arctic. Spread then took place westward along Arctic Russia to the White Sea. From the White Sea they were either "sluiced-up" in proglacial lakes or dammed in front of advancing pleistocene glaciers and carried into the Baltic. Or they may have migrated around Scandinavia to the Baltic while isotherms were depressed southward during glaciation. In either case, following deglaciation, the populations were left stranded in lakes and cooler portions on the Baltic to slowly undergo adaptation to higher temperature and lowered salinities, the intervening populations along the outer Norvegian coast disappearing. During the resultant isolation the present eperlanus type evolved. The origin of eastern North American mordax from western North American populations of the subspecies can be ascribed to a migration across Arctic Canada during a more recent interglacial period or during the warm postglacial hypsithermal period. Cooling them resulted in the present separation of populations. If the migration took place during an interglacial period, one may assume that intermixing took place during the hypsithermal thus preventing differentiation of east and west populations. Thus the two subspecies, one with disjunct distribution, can be readily derived. Range of mordax: South to Barkley Sound, Vancouver Island, British Columbia, in the east Pacific; south to Wonsan, Korea, in the West Pacific; in the Arctic east to Cape Bathurst, Northwest Territories, west to the White Sea. The northernmost point is on the southern island of Novaya Zemlya. In the Western Atlantic it is known from Pike Run Cove, Lake Melville, Labrador south to Delaware River, Pensylvania, and questionably to Virginia. Range of eperlanus: the Baltic and North Seas and their drainages, southward, including England to the mouth of the Loire River, France; upper Volga system" (McAllister, 1963). During the last 10-15 years small smelt have spread down the Volga River system to the Gorkov and Kuybishev waterbodies. (Kuznetzov, 1951; Kojevnikov, 1958).

Over its large range the smelt lives under various ecological conditions: salinity varies from oceanic to freshwater, temperatures vary from below 0°C (in winter) to + 20°C and higher (in summer). Land-locked forms of the smelt inhabit pure lakes, some over 30 m in depth, others shallow, with running water (Arnold, 1920), with high oxygen saturation, high pH (7.8-8.6 and more), high degree of mineralization and low oxidability (Petrov, 1940) and rich development of zooplankton (about 300-1300 mg/m^3). Kojevnikov (1955) found that the Finnish Gulf smelt migrates and spawns in rivers and estuaries at water temperatures from +2°C to 12-13°C. pH from 7.0 to 7.5, oxidability from 8.94 to 15.13 mg/l, concentrations of bicarbonates from 19.23 to 27.28 mg/l, oxygen about 100 percent saturated. In summer the smelt stays in open waters of the Finnish Gulf, below the epilimnion layer at temperatures about 5-7°C. In autumn the smelt stays at depths of at least 20 m, at water temperatures of 5-8°C, pH of 7.0-7.4, salinity of 3-4 °/oo. In winter the smelt stays at depths of 20-30 m, temperatures of + 2° and salinity of 5-6 °/oo. Generally the Finnish Gulf smelt spawns at temperatures from 5-6°C to 10-12°C, feeds at 5-10°C, spends the winter at +2°C. The White Sea smelt lives under more severe climatic conditions. The Sea covers with ice during 6-7 months of the year, the water temperature drops below zero. As the ice breaks the sea begins to warm and in summer the temperature of the surface layer rises to 16-18°C (and higher). The average salinity of the surface layers of the White Sea is 25-26 °/oo, of deeper layers 30-31 °/oo; it is lower near the river mouths (Onega, North Dvina and others). Subarctic populations of smelt inhabit waters with average zooplankton biomass of 50-400 mg/m^3 and average biomass of benthos of 4-30 g/m^2 (exoluding Mollusca and Echinodermata which the smelt does not feed on).

2.2 Differential distribution

2.21 Spawn, larvae and juveniles

The smelt spawns in rivers or near their mouths. Eggs are demersal, adhering to the substratum. When hatched, smelt larvae drift downstream where they are carried back and forth under the influence of the tide. Fingerlings stay offshore, feeding in pelagic waters in the same regions as adults.

2.22 Adults

The smelt stays near the shores for most of the year. It comes to the deeper waters of seas (or lakes) only in summer when shore waters become too warm. Smelt of all ages spend the winter in estuaries and mature fishes migrate upstream in spring.

2.3 Determinants of distribution changes

See 2.1, 3.16, 3.32

2.4 Hybridization

2.41 Hybrids; frequency of hybridization; species with which hybridization occurs; methods of hybridization

Interspecific hybridization is not known. Lillelund (1961) writes that experiments on fertilization and breeding of eggs from fast growing coastal smelt and slow growing smelt from fresh waters (inland lakes) have shown that it is possible to hybridize these two morphological races, which have been isolated since the Yoldia geological period. Evidently the data relate to migrant and landlocked smelt of Germany).

Fig. 9 Distribution of Osmerus eperlanus mordax-circles, and O.e.eperlanus-triangles.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.11 Sexuality

The smelt is normally heterosexual.

According to Hoffmeister (1939) about 3.7 percent of adult individuals of the Elbe river smelt are hermaphrodites (these individuals have male and female elements in the same gonads). According to Lillelund (1961), the figure for the same river is about 2 percent. These individuals do not lose the ability to reproduce. Hermaphrodite individuals occur more often among young smelt: Lillelund (1961) reports that 14 percent of the 0-group smelt of the Elbe river are hermaphrodites. Probably some of the hermaphrodites become males in the future. Hermaphroditism occurs more often in migrant smelt populations than in landlocked ones of West Europe (Hoffmeister, 1939). Hermaphrodites occur very rarely in the smelt populations of eastern Europe.

Sexual dimorphism is described by McAllister (1963) who states, "paired and anal fins slightly larger in males, large tubercles on scales; small ones on head and leading rays of dorsal, anal, caudal and paired fins in males. Tubercles reduced in females. There is a tendency in the males for a lateral muscular ridge to form, to be darker and to have a punctate operculum".

3.12 Maturity

The age at which sexual maturity is reached differs widely in different populations (Table VIII). Most smelt populations reach maturity at 2-3 years. The age of maturity gradually decreases on advancing from the northern part of East Europe eastwards to East Siberian shores. Some workers note that males reach maturity a year earlier than females, but others do not note such a difference.

Both sea and freshwater smelt populations are often biologically heterogeneous; there are ecological forms differing in size and rate of growth, age and size at maturity, period and place of spawning and other peculiarities. This holds true for the smelt populations of the Baltic Sea bays (Marre, 1931: Kojevnikov, 1955), lakes of East Europe (Arkhiptzeva, 1956; Stefanovskaya, 1957 and many others), and North American populations (Kendall, 1927 and others). The smaller and earlier maturing form is always non-migratory, the larger and later maturing one usually migrates for more or less considerable distances from feeding to spawning grounds. Existence of these ecological forms promotes the more complete use of food supply and spawning grounds.

Intensive growth during the first year of life is correlated with earlier maturity (lake populations of Europe and North America; populations which grow more slowly reach maturity later (Table VIII). Fast growing year-classes reach maturity earlier than those growing more slowly in the same population (Morosova, 1960; Lillelund, 1961; original data on White Sea smelt).

Size and weight at sexual maturity
See Table IX.

3.13 Mating

Each female usually spawns in the company of one male. The female extrudes her eggs, then leaves the spawning ground. According to Hoover (1936) and Lillelund (1961) an individual female may continue to spawn for several days, but the process is completed in several hours in White Sea smelt (original data). Males continue spawning with other females. Males spawn for a longer time and stay at the spawning grounds longer than females.

3.14 Fertilization

Fertilization is external.

3.15 Gonads

According to Kendall (1927) "... the gonads of the smelt are unsymmetrical organs, one on each side of the abdominal cavity. The organ of the left side is very much larger than that of the right and they are situated one behind the other. The left gonad is much larger in both sexes, the right being quite small and not far behind the outlet".

The correlation coefficients for different years between egg number and body weight in the White Sea smelt were +0.89 and +0.95, between egg number and body length +0.85 and +0.91 (Belyanina, 1966a). The egg number produced by a female increases with age; as a rule older fishes produce more eggs than younger fishes of the same size (Table X). Data on fecundity of various smelt populations according to size and age are given in Table XI and Table XII. Land-locked freshwater forms and Siberian populations have the lowest fecundity; migrant forms (White Sea, Baltic, Elbe river) have the highest fecundity.

Variability of relative weight of ripe ovaries (to body weight) in different smelt populations is rather small: from 18 to 22 percent (Table XIII). Weight of ripe testis is about 5 percent.

According to Lillelund (1961) for the Elbe river smelt:

$$y = 2.737x - 0.28637$$

where "y" = fecundity, "x" = body length

TABLE VIII

Sizes (cm) of fishes at successive years of life, age of maturation and age groups in spawning stocks in different smelt populations

Locality	Age groups 1	2	3	4	5	6	7	8	9	10	11	12	Age at first maturity	Age groups in spawning stock	Authority
Pskovsko-Chudskoye Lake	7.2	9.7	12.9										1	1-2	Fedorova, 1953
Ilmen Lake	4.7	8.2	10.7										1-2	1-3	Domrachev and Pravdin, 1926
White Lake	6.0	8.5	11.0										1-2	1-3	Fedorova, 1953
Rybinsk waterbody	5.9	8.7	9.4										1-2	1-3	Lapin, 1955-56
Dadey Lake	7.1	10.7	12.2										1	1-3	Willer, 1926
Lazmiaden Lake	8.2	9.3	11.8	12.7	15.6								2-3	2-5	Willer, 1926
Kurishes Haff:															
non migrant	6.3	10.5											1	1-2	Marre, 1931
sea migrant	6.5	13.3	16.1	20.4									2	2-4	Marre, 1931
Onega Lake	6.3	8.8	9.4	10.6	11.0	11.3	11.8	12.3					2-4	2-8	Stefanovskaya, 1957
Pyaozero (Karelia)			10.6	11.3	12.2	12.9	13.6	14.4					4-6	4-12	Melyantzev, 1946
Ladoga Lake	8.0	9.5	10.7	13.6	15.8	18.3							1-3	2-6	Arkhiptzeva, 1956
Elbe River	7.1	13.4	17.3	21.2	23.8								2	2-5	Lillelund, 1961
Neva River	7.8	11.1	13.6	16.0	17.6								3-4	3-9	Kojevnikov, 1956
Michigan	9.2	15.7	17.1										2	2-3	Creaser, 1929
Huron		13.7	15.5	18.3									2	2-4	Baldwin, 1948
Miramichi River		13.7	15.6	17.6	19.4								2	2-5	McKenzie, 1958, 1964
Basin of Maine		12.2	17.2	22.0	24.0								2-3	2-5	Rupp, 1959
White Sea:															
Onega Bay	4.7	10.1	14.5	19.2	23.2	27.4							2-4	2-7	Balagurova, 1957
Dvina Bay	4.1	9.3	13.2	16.9	19.1	21.5	24.6	27.4	28.1				3-4	3-9	Kirpichnikov, 1935
Kandalaksha Bay	4.7	12.9	18.8	22.6	25.0	27.0							3-4	3-5	Original
Chesha Bay	3.5	8.1	12.5	15.2	17.7	20.5	22.2						4-5	4-7	Kirpichnikov, 1935
Gulf of Ob				18.3	19.3	20.2	20.9	22.2					4-5	4-8	Amstislavsky, 1959
Yenisey River	4.6	9.8	14.1	17.6	20.3	22.3	23.9	24.4	25.5				5-6	5-9	Tyurin, 1924; Neiman, 1957
Lena River							19.6	23.4	26.3	27.6	28.8	30.1	7-8	7-12	Pirojnikov, 1950

TABLE IX

Size and weight at maturity (first spawning season) in different smelt populations

Locality	Length (cm)	Weight (g)	Authority
Rybinsk waterbody	6.0-9.0	1.9-6.2	Lapin, 1955-56
White Lake	6.0-8.5	1.5-3.5	Schetinina, 1954
Ilmen Lake	4.7-8.2	1.1-4.3	Domrachev & Pravdin, 1926
Lazmiaden Lake	9.3-11.8	5.1-8.5	Willer, 1926
Kurishes Haff	6.3	1.4	Marre, 1931
Ladoga Lake	8.0-11.0	3.3-8.7	Arkhiptzeva, 1956
Onega Lake	8.8-10.6	3.7-6.1	Stefanovskaya, 1957 and others
Elbe River	16.5-18.2	abt.17	Lillelund, 1961
White Sea	18.8-22.6	41.7-75.5	Original
Ob River	18.3-19.3	42.5-48.5	Amstislavsky, 1959
Yenisey River	20.3-22.3	51.2-68.0	Tyurin, 1924 and others
Lena River	19.6-23.4	53.0-94.0	Pirojnikov, 1950
Upper Lake	14.0-16.0	17.0-25.5	Bayley, 1964

TABLE X

Fecundity (thousands of eggs) of females of the same sizes but different ages (White Sea smelt, original data)

Length (cm)	Age groups					
	3		4		5	
	Average	min.-max.	Average	min.-max.	Average	min.-max.
19.0-19.9	37.6	25.6-44.5	42.0	37.1-50.0	-	-
20.0-20.9	53.0	45.5-61.0	53.2	40.7-66.3	-	-
21.0-21.9	52.8	-	62.1	43.9-83.8	-	-
24.0-24.9	-	-	88.6	87.7-90.0	95.5	88.8-102.3

Number of eggs per 1 g of body weight of one female is given in Table XIII. Siberian smelt populations have the lowest value of this character, the Pskov lake smelt have the highest.

The smelt spawns once a year, so the number of eggs produced by a female during a year may be found in Table XII. Small smelt (Pskov-lake, Ilmen lake etc.) spawn once only (Lapin, 1960; Kuznetsov, 1964). Migrant sea populations have a longer life cycle; most White Sea smelt spawn once or twice during their lives and some spawn three times (Belyanina, 1966a). Siberian smelt apparently may spawn more often, but there is some evidence that such fish do not spawn every year (Kravchuk, 1958). The number of eggs produced by an individual during a lifetime may be calculated from Table XII. Belyanina (1966b) reported that White Sea smelt contained less fat and had lighter gonads, lower fecundity and smaller eggs after the heavy winter of 1960-61 than after the good winter of 1961-62 (Table XIV).

According to Lillelund (1961) the yield of different year-classes in the Elbe river shows a positive correlation with the water level and is affected by temperature and food conditions during the four weeks after hatching. Some workers note that the yield tends to increase in colder years.

3.16 Spawning

The smelt spawns once a year as a rule but Kravchuk (1958) noted that some Siberian smelt do not spawn every year.

Sometimes smelt spawn under ice. In most areas spawning continues for about one month, but peak spawning usually lasts only 2-4 days;

TABLE XI

Fecundity of different smelt populations (thousands of eggs)
Data grouped by length groups

Locality	Length groups (cm) 6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	Authority
Pskovsko-Chudskoye L.	2.1	2.8																							Lapin's unpublished data
Uchinskoye waterbody					7.7																				Spanovskaya & Grygorash, 1963
White Lake	1.7		3.2		4.6																				Fedorova, 1953
Rybinsk waterbody		2.6			5.5			13.5																	Schetinina, 1954
Kurishes Haff (small)	1.4	1.7		2.6																					
Pyaozero							2.9	5.8	6.4	15.1	20.1			45.6	48.5										Marre, 1931
Onega Lake				2.9	3.7	5.5	8.6																		Melyantsev, 1946
Ladoga Lake				2.9	4.5	5.6	7.5	9.5	11.8	19.0	22.4	24.8	27.9	31.3	34.5	44.5	61.2								Alexandrova, 1963
Kurishes Haff (sea-migrant)						5.3	7.8	11.2	16.1	17.0	19.7	24.4	26.1	31.3	36.7		41.9								Markun, 1926; Arkhiptzeva, 1956
Neva River							10.9	12.2	13.6	16.1	16.1	25.4	30.8	35.0	33.9	41.5	45.2	45.5		68.5	93.5				Marre, 1931
Finnish Gulf					5.3	6.4	9.8	12.7	16.7	19.5	23.6	31.9	33.6	41.9											Kojevnikov, 1949
Elbe River							6.5	8.0	12.0	14.5	18.0	22.5	28.0	35.0	38.0	45.0									Lapin's unpublished data
White Sea: Kandalaksha Bay												30.1	32.9	35.8	49.6	61.4	72.0	80.5	83.5	114	124	137	140	161	Lillelund, 1961
Onega Bay								9.1	12.7	16.9	18.6	25.1	32.9		35.9	49.5	54.5	55.0	65.4	47.3					Original data after Balagurova, 1957
Gulf of Ob													15.5	16.3	22.8	25.0									Amstislavsky, 1959
Yenisey River																		37.4	48.7	54.1					Tyurin, 1924; Neiman, 1957

TABLE XII

Fecundity of different smelt populations
(data grouped by age-groups and given in thousands of eggs

Locality	Age groups 1	2	3	4	5	6	7	8	9	10	11	12	Authority
Pskovsko-Chudskoye Lake	2.6	2.7	-	-	-	-	-	-	-	-	-	-	Lapin's data
White Lake	1.7	3.2	4.6	-	-	-	-	-	-	-	-	-	Fedorova, 1953
Rybinsk waterbody	2.6	5.7	13.6	-	-	-	-	-	-	-	-	-	Schetinina, 1954
Pyaozero (Karelia)	-	-	-	2.9	-	5.9	6.3	18.0	-	-	45.6	48.5	Melyantzev, 1946
Onega Lake	-	-	2.9	3.7	5.5	8.6	-	-	-	-	-	-	Alexandrova, 1963
Kurishes Haff	-	9.6	19.9	33.1	41.9	-	-	-	-	-	-	-	Marre, 1931
Finnish Gulf	-	6.7	13.4	24.7	25.0	-	-	-	-	-	-	-	Lapin's data
Elbe River	8.0	21.0	37.5	-	-	-	-	-	-	-	-	-	Lillelund, 1961
White Sea:													
Kandalaksha Bay	-	-	35.6	69.6	126.1	133.6	-	174.0	-	-	-	-	Original data
Onega Bay	-	10.6	22.9	39.5	60.1	-	-	-	-	-	-	-	Salagurova, 1957
Gulf of Ob	-	-	12.5	15.9	20.9	25.5	31.5	-	-	-	-	-	Amstislavsky, 1959
Yenisey River	-	-	-	-	-	-	37.4	48.7	54.1	-	-	-	Tyurin, 1924, Neiman, 1957

TABLE XIII

Egg number per g of body weight, size of ripe eggs and relative weight of gonads (as % of body weight) in different smelt populations

Locality	Egg number per g of body weight	Average diameter of egg (mm)	Relative gonad weight	Authority
Pskovsko-Chudskoye Lake	1050	0.55-0.75	18.4	Lapin's data Kuznetzov, 1964
White Lake	580	0.85-0.90	-	Fedorova, 1953 Schetinina, 1954
Rybinsk waterbody	710	0.70-0.90	20.7	Lapin's data Schetinina, 1954
Pyaozero (Karelia)	560	0.79	13.5	Melyantzev, 1946
Ladoga Lake	610	0.80	18.2	Markun, 1926 Arkhiptzeva, 1956
Kurishes Haff	665	0.82	-	Marre, 1931
Finnish Gulf	630-700	0.75-0.95	18.1	Lapin's data Kojevnikov, 1949
Elbe River	650	0.70-0.90	18-19	Lillelund, 1961
White Sea:				
Kandalaksha Bay	700	0.86-0.94	22	Original data
Onega Bay	710	0.77	22	Balagurova, 1957
Ob River	350	1.06	18-20	Amstislavsky, 1959
Yenisey River	370	0.96	20	Tyurin, 1924
Suyfun (Far East)	530	-	18.4	Dulkeit, 1937

TABLE XIV

Comparison of fecundity of females of the same weight in 1961 and 1962 (White Sea, original data)

Characters	Weight (without internal organs) (g)					Number of fishes
	30 - 45	45 - 60	60 - 75	75 - 90	90 - 105	
1961 Fecundity (thousands of eggs)	33.5	42.5	66.1	74.9	86.6	100
Egg number per g of body weight	884	862	947	927	910	
Average weight of gonads (g)	10.1	11.3	22.8	23.1	27.3	
Average diameter of an egg (mm)	0.83	0.79	0.87	0.87	0.85	
Fatness (% of wet weight)	1.7-2.1					
1962 Fecundity (thousands of eggs)	36.5	48.6	68.6	78.0	99.2	204
Egg number per g of body weight	893	913	1008	980	1016	
Average weight of gonads (g)	11.2	15.7	21.9	25.1	33.4	
Average diameter of an egg (mm)	0.91	0.92	0.92	0.92	0.93	
Fatness (% of wet weight)	2.9-3.0					

TABLE XV

Spawning seasons of smelt in different areas

Area	Spawning season	Authority
West Europe	March	Lillelund, 1961
Baltic and drainage	April - May	Probatov, 1927 and others
Upper Volga system	April - May	Fedorova, 1953 and others
White Sea, Karelia	May, early June	Melyantzev, 1946; Balagurova, 1957, and many others
Siberia, Far East	June, early July	Agapov, 1941; Amstislavsky, 1963; Ivanova, 1955; Kuznetzova, 1962
Atlantic coasts of North America	From February (the south boundary of the area) to the beginning of June (the Miramichi River and northwards)	McKenzie, 1964

according to McKenzie (1964) in the Miramichi river it lasts 5-10 days. There may be several spawning peaks, depending on weather conditions and population heterogeneity (subpopulations).

As a rule smelt spawn at night (Domrachev and Pravdin, 1926; Kendall, 1927, Hoover, 1936; Lievense, 1954, Rupp, 1959, McKenzie 1964, and original data).

The majority of workers have noted a decrease in the size of smelt during the spawning run: the older and larger individuals spawn first. Changes in the sex-ratio on the spawning grounds are discussed below.

According to Rupp (1959) the character of the spawning run depends on ice conditions: the spawning run of smelt in Maine, U.S.A. (in 80 percent of cases) begins within the first 10 days after the ice has broken. The spawning run breaks off when the weather is stormy or the moon is very bright. Colour of water does not influence the spawning run.

All over its great range(see Table XV) the smelt begins to spawn when the water temperature is about +4°C (sometimes 1-2° lower or higher). The spawning peak occurs at water temperatures of 6-9°C (Chumayevskaya-Svetovidova, 1945; Marcotte, 1946; Marcotte and Tremblay, 1948; Dryagin, 1949; Schetinina, 1954; Ivanova, 1955; Stefanovskaja, 1957; McKenzie, 1964, etc.). Spawning breaks off at a sharp decrease in water temperature. It lasts longer in cold years than in warm ones. The spawning smelt usually avoids temperatures lower than 4°C and higher than 12°C. Spawning begins earlier in warm years with high water level. The smelt enters rivers and spawns at high tide. Sometimes the spawning run is delayed because of ice movements.

Esox lucius, Leuciscus idus, Rutilus rutilus, Misgurnus fossilis, Acerina cernua spawn almost at the same time as smelt in fresh waters of eastern Europe (Meshkov and Sorokin, 1952).

As a rule smelt ascend rivers to spawn (see 3.51), but some freshwater smelt populations spawn near river mouths and do not ascend the rivers (Melyantzev, 1946; Fedorova, 1953; Schetinina, 1954, etc.). Many authors note that water depths at smelt spawning grounds vary from several centimetres to several metres. According to Stefanovskaya (1957) smelt eggs occur at the depths of 17 m in some Karelian lakes. The eggs are deposited on stones, pebbles, water plants, submerged parts of bushes, grass and other things. They do not occur on muddy bottoms. The current velocity in the spawning grounds of the White Sea smelt is between 0.3 and 2 m/sec (original data).

Spawning areas are larger in the years with high water level. Rupp and Redmond (1966) noted that smelt taken from spawning grounds in rivers and introduced into some lakes of Maine did not enter other rivers but spawned near the banks of the lakes.

A number of authors, including Kendall (1927), Baldwin (1948), Lillelund (1961), Amstislavsky (1963), and unpublished data re-

lating to the White Sea show that at the beginning of the spawning season females are more numerous than males (about 70 percent in the White Sea smelt). At the height of the spawning season the sex ratio becomes 1:1, then the number of females continues to decrease and at the end of the spawning season males dominate (about 90 percent in the White Sea smelt). Some workers (Stefanovskaya, 1957; Alexandrova, 1963) note the inverse phenomenon. McKenzie (1964) found that the sex ratio during the spawning run varied from place to place and time to time. In the Miramichi river, New Brunswick, Canada, at the beginning of the run in March and April about 60-70 percent of the smelt were males. "These percentages declined during late April and early May to 50 percent and 25 percent and increased again in late May and early June to 55 percent and 70 percent males... After 1-3 days of spawning during which smelt are only in the brooks during the night, some smelt remain in the brook all day... They are almost all males, but as the season advances this percentage declines, then at the end of the season, increases again. In the evening the number of females increases as smelt enter the spawning streams. Two or four hours after dark females comprise 50-75 percent of the fish in the spawning stream. From that time until daylight many smelt return to the river leaving a higher percentage of males in the brooks again. This behaviour has been reported by Greene (1930), Langlois (1935), Hoover (1936) and Van Oosten (1940). Above the head of tide in the main branches of the Miramichi where the rivers are wide and deep there are also nightly movements of females into the shoal water close to shore where the proportion of females increases from about 15 - 50 percent between dark and midnight. From about 3 a.m. the percentage of females declines again to about 15 percent by daylight leaving males dominant in the shoal water along shore" (McKenzie, 1964).

According to Hoover (1936) individuals of the same sex touching each other separate in a moment while individuals of different sexes form a spawning pair. Evidently the sexual dimorphism (large tubercles on scales in males See 3.11) plays an important role. Each female spawns with one male who stays a little above and ahead of the female. Both extrude their reproductive products in small portions.

Marcotte (1946) states that smelt spawning in the St. Lawrence River are more sluggish at the water temperature of 5-6°C than at higher temperatures.

The smelt does not make nests and does not guard eggs and larvae. Fertilized eggs adhere to the substratum. Egg density varies greatly and relates to spawning conditions, size of spawning ground, presence of suitable substratum, number of spawning individuals. According to Rothschild (1961) the average egg density on the smelt spawning ground in the Dean-Brook river is 6 eggs/cm^2. There is a positive relation between the egg survival and the distance from the mouth of the river. Amstislavsky (1959) stated that smelt eggs in the Saletta river (the Gulf of Ob) spread to a distance of 0.3-0.5 cm from each other; sometimes groups of 5-15 eggs occurred. According to Rupp (1959) the eggs of freshwater smelt in the basin of Maine are laid in a patch 3-6 m long. The eggs of the White Sea smelt spread irregularly, often in clumps; along the shores their density reaches 1000 eggs/cm^2, while there are only 4-6 eggs/cm^2 on stones in currents (original data). The average density of eggs of the White Sea smelt was 30-50 eggs/cm^2 on one spawning ground and 240 eggs/cm^2 on another. According to McKenzie (1964) the layer of smelt eggs in the Miramichi River reaches a thickness of 10 cm. Evidently it is because of the small size of the smelt spawning grounds. The areas of four spawning grounds of the White Sea smelt were 400, 150, 50 and 500 m^2 (original data); the spawning ground of the Ilmen lake smelt has a total area of about 2000 m^2 (Domrachev and Pravdin, 1926), while that of the Neva River smelt is less than 5 km^2 (Kojevnikov, 1955).

Rupp (1959) stated that geographical isolation of different smelt populations results in some genetic differentiation and specialization. A study of the results of experimental introduction of smelt into the waters of Maine led Rupp and Redmond (1966) to suggest that the time of spawning is genetically controlled and may lead to the reproductive isolation of subpopulations inhabiting the same waterbody.

3.17 Spawn

Sizes of ripe eggs vary in different smelt populations (Table XIII). The small smelt of Pskov lake have the smallest eggs, the smelt of the Ob and Yenisey Rivers have the largest. Smelt eggs are round or slightly oval, yellowish-white to yellow. Unfertilized eggs are semi-transparent, with many oil globules. Egg membranes are described in Section 1.32.

After extrusion the egg is rolled by the current and will stick to any substratum. The outer coat of the egg becomes viscous in 15-20 sec after extrusion in water (McKenzie, 1964). Soon after sticking to the substratum the outer coat bursts open, slips down and becomes free from the inner one except at one point. This point is the micropyle. So the egg develops swaying in the current. Some of the eggs become detached and float with the help of the outer coat (Ehrenbaum, 1894; Marre, 1930; Tremblay, 1946; Balagurova, 1957). Some workers (Chumayevskaya-Svetovidova, 1945; Grib, 1946 and some others) consider this pelagic phase as obligatory in the development of smelt eggs. How-

ever according to Unanyan and Soin (1963) only dead eggs of the White Sea smelt become detached from the substratum.

The vitellus is round or a little oval in shape. A thin layer of cytoplasm surrounds it. The vitelline membrane is thin, and numerous oil globules are dispersed all over the vitellus (see 1.32).

3.2 Pre-adult phase

3.21 Embryonic phase

The embryonic phase is described by Unanyan and Soin (1963). After extrusion into water, the egg immediately swells. Its diameter increases about 0.2 mm, perivitelline space forms between the vitellus and the membranes. In 4 h (temperature of 8.5°C) the blastodisc forms at the animal pole of the egg (Fig. 10.1). In 8 h after fertilization 2 blastomeres are present (Fig. 10.2); in 13 h 30 min, 8 blastomeres are present (Fig. 10.3). In 2.5 days after fertilization (12°C) the blastula has formed (Fig. 10.6). Formation of the embryonic plates begins 2 days 14 h after fertilization (Fig. 10.7). In 3 days gastrulation is complete (Fig. 10.8). In 4 days 5 h (10.5°C) the embryo has eyecups (Fig. 11.3, 4); in 5 days 5 h after fertilization (10°C) segmentation of the mesoderm begins, the main parts of the brain form, auditory vesicles and crystalline lenses in the eyes are present. The embryo has a chorda, 30-32 myotomes, and the caudal part begins to separate from the yolk sac (Fig. 11.5,6,7). In 7 days 10 h the embryo has a long tail separated from the yolk sac, the eyes have developed black pigment; the embryo shows twitching movements within the egg (Fig. 11.8). In 9 days and 16 h after fertilization (9.5°C) hatching glands are present all over the body surface, particularly on the head and pectoral fins; the parts of the brain are well formed; the black pigment in the eyes become stronger and yellow pigment appears. The yolk sac is egg-shaped. The embryo has olfactory vesicles; semicircular canales are present in the auditory vesicles. The head is not distinct from the yolk sac. The mouth is at the lower side of the head. Four rudimentary gill slits and a rudimentary operculum are present. Melanophores are found on the ventral side of the caudal myotomes, under the alimentary canal, and on the yolk sac. The heart pulsates regularly; it consists of two chambers. The blood has no corpuscles. There are 42 pre-anal and 17 post-anal myotomes (Fig. 12-1).

During embryonic development there are no differences between migrant and small freshwater smelt except the body size and number of myotomes (Grib, 1946).

Egg predators include insects and fishes (sticklebacK, smelt itself and others). Eggs may become parasitized by Saprolegnia.

Many authors (including Schneberger, 1937; Meshkov and Sorokin, 1952; Unanyan and Soin, 1963) have remarked on the high rate of survival of smelt eggs during incubation. According to Lillelund (1961) the rate of mortality increases only at the end of the incubation period, when about 86 percent of eggs of the Elbe river smelt die. However Rothschild (1961) has stated that loss of smelt eggs in the Dean-Brook river, Maine, U.S.A., is 99.5 percent. The main causes are drying after the water level has dropped, overwarming and predation (see above). Influence of these factors is least in cold years with high water level.

Rothschild (1961) and McKenzie (1964) found that the number of larvae produced per unit area increases up to egg densities of about 11-13 per cm^2 and declines when the density of eggs is higher. The relative larval production is highest (hatching rate 3.6%) when the average density of eggs is 0.5 per cm^2 and declines to 0.03% at an egg density of 194 per cm^2.

Before hatching, the embryo begins to move very energetically, the caudal part moving especially sharply. The membrane bursts and the tail comes out first. Moving energetically the embryo frees itself, the egg-case remains on the substratum or is torn off during hatching.

3.22 Larval phase

The period of incubation varies in different smelt populations (Table XVI). Generally small forms have a shorter period of incubation and the newly hatched larvae are smaller. Naturally the sum of day-degrees from fertilization until hatching is not constant, but increases exponentially with decreasing water temperature.

A newly hatched pro-larva has the yolk sac about 0.7 mm in length. There is an oil globule in it. The globule resolves after the yolk. Grib (1946) described 4 stages in the larval development of the Neva river smelt:

1. Pro-larva with yolk-sac. This stage lasts 7-9 days. The dorsal fin fold begins at the second segment. The pre-anal fin is well developed. Pectoral fins are present. Pigmentation is on the ventral part only. The body is transparent. The blood has no corpuscles. The mouth becomes terminal at the end of the stage. The pro-larva begins feeding while the oil globule is still present. The pro-larva measures to 7 mm in length (Fig. 12-2,3).

Fig. 10 Early stages of development of eggs of the White Sea smelt (to the end of gastrulation) (from Unanyan and Soin, 1963).

Fig. 11 Late stages of development of eggs of the White Sea smelt (to hatching) (from Unanyan and Soin, 1963).

TABLE XVI

Duration of period of incubation and body length at hatching in different smelt populations

Locality	Sum of day-degrees	Body length at hatching (mm)	Authority
Pskov-lake	80	3.8	Meshkov and Sorokin, 1952
Valday-lake	110	6.2	Chumayevskaya-Svetovidova, 1945
Rybinsk-waterbody	138	4.2-4.9	Schetinina, 1954
Elbe river	60-110	5.0-6.0	Lillelund, 1961
Neva river	140-180	5.4-6.0	Grib, 1946
White Sea	abt.170	6.0	Unanyan and Soin, 1963
Ob estuary	132	-	Amstislavsky, 1959
Miramichi river	174	5.0	McKenzie, 1964

2. Larva without yolk-sac, 6.8-13.4 mm. Blood corpuscles are present. The fin fold is reduced, dorsal and anal rays are developing. Pigmentation is similar to that of the pro-larva; a pigment spot of two melanophores is present under the anus. The alimentary canal is tubular. A rudimentary gas-bladder can be seen at the end of the stage. This stage lasts from 10-14 days after hatching (Fig.13).

3. Larvae of 13-18 mm. The body is transparent. The dorsal, anal and adipose fins have formed. Rays are present in the unpaired fins. The caudal fin is rounded. The pre-anal fold begins from the eighth pre-anal segment.

4. Larvae of more than 18 mm (28 mm in average). Such larvae appear in the Neva river in July-August. The caudal fin is indented. The final number of rays are present in the dorsal and anal fins. The embryonic fin fold can be distinguished on the ventral side in fish of up to 30 mm. The ventral fins are situated more posteriorly than earlier as a result of growth of the gas bladder. Upper and lower vertebral arches are present. The operculum covers the gills completely. Pigment is concentrated mainly on the ventral side. Melanophores appear on the operculum, on the top of snout, under the eyes, along the chorda, on the body sides and on the dorsal part of the tail to the end of the stage. Larvae and adults have similar meristic and plastic characters. The number of myotomes does not change during the larval period.

According to Rass (1949) in general the smelt larvae belong to the "herring type" having a relative short caudal part, isometric pigmentation, low disposition of the pectoral fins, homocercal tail and so on.

Smelt eggs and larvae are fed on by the three-spine stickleback, gobiids, herring, perch and other fishes (including the smelt itself) and larvae of Insecta. One of the main causes of egg mortality is Saprolegnia.

Unanyan and Soin (1963) stated that larvae of the White Sea smelt begin to take food within 6 days of hatching and are entirely dependent on external feeding 9 days after hatching. According to Grib (1946) the Neva river smelt begins to feed 7-9 days after hatching. The corresponding time for Pskov-lake smelt is 7-8 days (Meshkov and Sorokin, 1952).

Lillelund (1961) stated that a pro-larva with yolk-sac may live without feeding for 10-14 days at a temperature of 10-12°C.

Larval smelt feed on small planktonic forms: young stages of Copepoda and Rotatoria, larvae of Gastropoda and Lamellibranchiata.

3.23 Adolescent phase

According to Grib (1946) the adolescent phase in the Neva river smelt begins in August-September when the first scales form (age 4 mo). Ehrenbaum (1909) gave the same data for the Elbe river smelt. However McKenzie (1958) stated that first scales in the Miramichi river smelt form at a length of 20-25 mm (age 2 mo). By this time the pigmentation of the dorsal part becomes more intense.

The main mortality occurs during the first months of life. Lillelund (1961) found that the mortality coefficient is the highest from May-August, its value decreases to October and then it is of little importance.

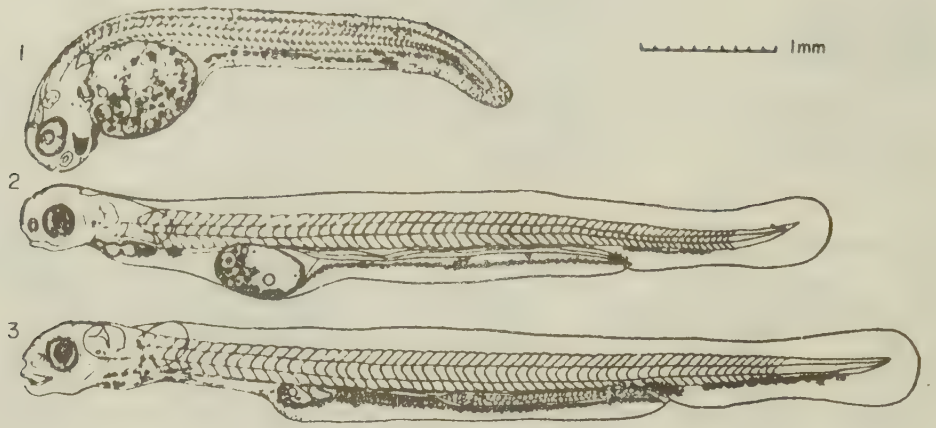


Fig. 12 1. Embryo of White Sea smelt, egg-membranes removed

2,3. Prolarvae of White Sea smelt (from Unanyan and Soin, 1963)

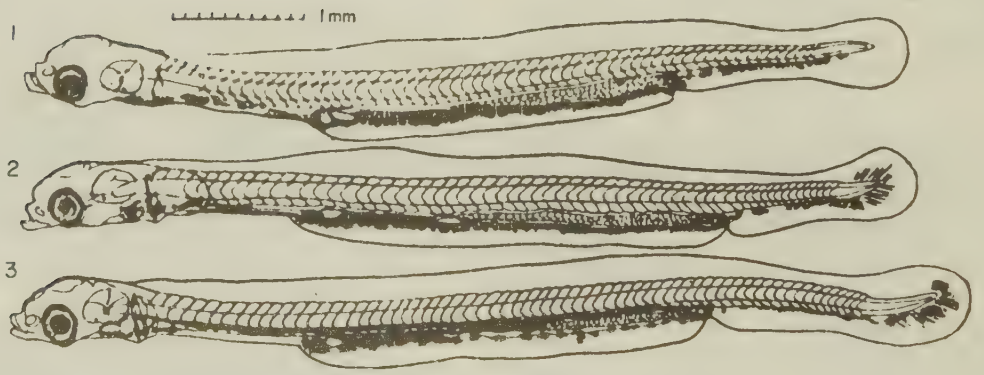


Fig. 13 Larvae of White Sea smelt after resorbtion of yolk (from Unanyan and Soin, 1963)

The young smelt feeds on planktonic crustaceans (Copepoda, Cladocera) and other groups of zooplankton.

3.3 Adult phase (mature fish)

3.31 Longevity

Longevity varies greatly in various populations of Osmerus eperlanus (Table VIII). Generally small freshwater smelt do not survive for more than 3 years. Individuals of 12 and even 15 years old may be found in the smelt populations of estuaries of the Yenisey, Lena, Anadyr and Khatanga rivers (Agapov, 1941; Mikhin, 1941; Lukyanchikov, 1964). The maximal age of males is usually 2 years less than that of females.

3.32 Hardiness

The environment of smelt populations is discussed in section 2.1.

According to Lillelund (1961) experiments made in Hamburg harbour showed that eggs develop in spite of sewage water. Only in the last phase of development where there is very little current is there a great mortality of eggs, caused by the accumulation of detritus, protozoa and algae on the eggs. Eggs of smelt are fertile up to a salinity of 16 °/oo. The susceptibility of eggs to salinity during the period of incubation depends on the stage of embryological development. A salinity below 10 °/oo is neither injurious to eggs nor to larvae. The upper limit of temperature tolerance of early eggs lies in the range 17.7-20.7°C, for later stages it is 21-24°C. Comparable data for adult smelt are not available.

3.33 Competitors

The main food competitors of Siberian smelt are Coregonidae and Acerina cernua feeding on Chironomidae larvae and nektobenthic Crustacea (Pirojnikov, 1950, 1955; Amstislavsky, 1963, and others).

Young of the White Sea smelt compete for zooplankton with herring, adults compete for Amphipoda, Mysidacea and some Cumacea with herring in April-May and September-October (Epstein, 1957). There is great similarity in diet (especially on the basis of Polychaeta) between the White Sea smelt and Eleginus navaga, Myoxocephalus scorpius, M. quadricornis (Russanova, 1963), Gasterosteus aculeatus (Timakova, 1957), Pleuronectes flesus and Liopsetta glacialis (Kudersky and Russanova, 1963). According to Abdel-Malek (1963) there is no food competition between adults of smelt and three-spined stickleback. In the early summer the Finnish Gulf smelt competes for planktonic crustaceans with young and partly adult Cyprinidae (Rutilus rutilus, Alburnus alburnus, Abramis brama, Leuciscus idus and others) and perch (Perca fluviatilis) (Kojevnikov, 1955). The young of the Elbe river smelt compete for food with the young of Clupea finta from May to August (Lillelund, 1961). The fresh water smelt of the north-western part of USSR occupies the food niche of a plankton-feeder in open waters and competes for zooplankton with Coregonus albula, Abramis ballerus, Alburnus alburnus, young of Perca fluviatilis, sometimes with Rutilus rutilus and Acerina cernua (Petrov, 1940; Meshkov and Sorokin, 1952, and others).

3.34 Predators

Sea mammals, birds and fishes (cod in particular) feed on migrant spawning smelt in subarctic waters. Esox lucius, Lucioperca lucioperca and large individuals of Perca fluviatilis feed on smelt in European fresh and brackish waters. Salvelinus fontinalis, Cristiwomer namaycush, Coregonus clupeaformis, Stizostedion vitreum, Perca flavescens, Anguilla rostrata, Micropterus dolomieu, Morone americana and Lota maculosa feed on smelt in North American waters (Kendall, 1927).

There is some evidence that the specific smell of smelt stock scares away other fishes.

3.35 Parasites, diseases, injuries and abnormalities

According to Petrov (1940) 28.5-36.6% of the Pskov-lake and 20% of the White lake smelt are parasitized. Parasitism is less intensive in other lakes of West Europe. Shulman and Shulman-Albova (1953) list 16 species of parasites for the White Sea smelt.

The list of smelt parasites recorded from waters of the USSR is given in Table XVII

3.4 Nutrition and growth

3.41 Feeding

Amstislavsky and Brussynina (1963) stated that the Ob river smelt feeds during day and night but with different intensity: maximum feeding takes place at 13 and 21 h corresponding to vertical migration of zooplankton; minimum feeding is at 5 h.

Migrant smelt feeds in coastal and offshore waters of seas and in river estuaries; landlocked forms feed in open waters of lakes.

The smelt searches in the water taking food organisms selectively (Table XVIII).

According to Timakova (1957) the White Sea smelt feeds on fish (herring) and Crustacea during the post-spawning period. Intensity of

TABLE XVII

Parasites of smelt (for territory of USSR)[1/]

Class or Order	Species	Stage of parasite infecting smelt	Infected organs	Other hosts and stages in them	Area
Microsporidia	Glugea herwigi* Weissenberg, 1921	Adult	Muscles, gills, mesenteries, etc.		Baltic, White and Barentz Seas and their basins, lakes of the Upper Volga, Amur.
Cestoidea	Triaenophorus crassus Forel, 1880	Larva (pleurocercoids)	Muscles and internal organs	Procercoids in body cavity of Copepoda, adult is a parasite of pike	Area of Esox lucius and Esox reicherti
	Triaenophorus* nodulosus (Pallas, 1781)	Larva (encysted pleurocercoids)	Liver and other organs	Any Copepods, the final hosts are pike, perch and other predators	All over USSR
	Eubothrium crassum Bloch, 1779	Adult	Intestine	Pleurocercoids in intestine of perch, procercoids in any Cyclops	Within the ar area of Salmonids
	Dyphyllobothrium latum (L.,1758)	Larva (pleurocercoids)	Muscles, liver and other organs	The final host-mammals	North-Western USSR, Volga Yenisey, Ob Rivers, basins
	Diphyllobothrium norvegicum Vik, 1957	Encysted Pleurocercoids	Tissues of intestine and stomach	Final hosts mammals and birds	Not recorded
	Proteocephalus longicollis (Leder, 1800)	Adult	Intestine		North-Western USSR, Siberia Kamchatka, Amur River
Trematoda	Leicithaster sp.	Adult	Intestine		Not recorded
	Orientophorus petrovi (Layman, 1930)	Adult	Pyloric caeca		Far East, Kamchatka
	Podocotyle reflexa (Creplin, 1925)	Adult	Intestine		Basins of the White, Barentz, Japan Seas

1/ Table based on "A key for identification of parasites of freshwater fishes of USSR", edited by B. Byhhovsky (1962)

TABLE XVII (continued)

Class or Order	Species	Stage of parasite infecting smelt	Infected organs	Other hosts and stages in them	Area
Trematoda	Bucephalus polymorphus Baer, 1827	Adult	Gill tissues, under skin		Baltic and White Seas basins, Siberian and Far East Rivers
	Cotylurus pileatus (Rud., 1802)	Cysts	Tissues of gas bladder and other internal organs, body cavity	Final hosts-birds	Baltic and White Sea, Volga Siberian Rivers Rybinsk waterbody, Karelia
	Tetracotyle ** intermedia Hughes, 1928	Larva	Heart	Adult unknown	Not recorded
	Diplostomum *** spathaceum (Rud., 1819)	Larva	Crystalline lens of eyes	Final hosts-birds	Not recorded
Nematoda	Contracaecum aduncum (Rud., 1802)	Adult Larva	St mach, oesophagus, pyloric caeca Liver, mesentery, muscles		North-Western USSR, Ob and Amur Rivers, Japan and Okhotsk Seas. basins
	Porrocaecum eperlani (Linstow,1879)	Adult, larva	Dorsal muscles under skin		North-Western USSR
	Cystidicola farionis Fisher, 1798)	Adult, larva	Gas bladder		Baltic, White, Barentz, Bering Seas basins
	Camallanus lacustris (Zoega, 1776)	Adult, larva	Intestine		Everywhere, except the Amur River basin
	Camallanus truncatus (Rud., 1814)	Adult, larva	Intestine		Everywhere, except the Amur
	Philometra sanguinea (Rud., 1917)	Adult, larva	Body cavity, the skin between fin rays		Not recorded

TABLE XVII (continued)

Class or Order	Species	Stage of parasite infecting smelt	Infected organs	Other hosts and stages in them	Area
Acantocephala	Echinorhynchus gadi Müller, 1776	Adult	Intestine	Not shown	Not recorded
	Pseudoechinorhynchus clavula (Dujardin, 1845)	Adult	Intestine	Intermediate hosts-Gammarus pulex and Pontoporeia affinis	Everywhere
	Metechinorhynchus salmonis (Müller, 1780)	Adult	Intestine	Intermediate host-Pontoporeia affinis	
	Pomphorhynchus laevis (Müller)	Adult	Intestine, liver	Gammarus pulex	North-Western USSR, Volga
	Corynosoma semerme (Forssell, 1904)	Larva	Body cavity	Final hosts - sea mammals rarely birds	North and East Seas of USSR
	Corynosoma strumosum (Rud., 1802)	Larva	Body cavity, muscles, internal organs	Final hosts - sea mammals rarely birds	North and East Seas of USSR
Copepoda	Ergasilis briani Markewitsh, 1932	Adult	Gills		Baltic, Siberia, Amur River
	Ergasilis sieboldi Nordmann, 1832 *	Adult	Gills		Baltic, Japan Sea Siberia
	Caligus macarovi Gussev 1951	Adult	Gills, skin		Far East
Branchiura	Argulus foliaceus (L.,1758) *	Adult	Gills and skin		Europe, Siberia

* May cause mass mortality of fish
** Causes loss of weight
*** Causes blindness and mortality

TABLE XVIII

Selection of food organisms by the Lena river smelt (after Pirojnikov, 1955). Fishes were 6-11 years old and measured 161-317 mm

Components	share (in %) in plankton	in nekton	Share in the diet of smelt
Copepoda	51.2	-	0
Cladocera	32.9	-	0
Mysidae	-	24.2	67.3
Amphipoda	-	11.9	11.4
Isopoda	-	1.7	0
Cumacea	-	7.0	0

feeding increases until July. Polychaeta (45%) and herring eggs (27%) are the main food components. In summer older individuals feed on Polychaeta, Decapoda and fishes, in autumn they feed on Polychaeta and Amphipoda. Intensity of feeding decreases until December. In winter it is low, and food consists of nektobenthic Crustacea. Amstislavsky and Brussynina (1963) noted that the Ob river smelt feeds on Amphipoda in winter. During the vegetative season Mysidacea, Copepoda, Cladocera and young smelt are important in smelt diet. The Lena river smelt has the same diet (Pirojnikov, 1950, 1955). The Elbe river smelt feeds on Eurytemora from April to October and Gammaridae from November to March (Ladiges, 1935). Planktonic Crustacea dominate in the diet of small freshwater smelt. Their importance in the diet depends on seasonal abundance.

According to Timakova (1957) intensity of feeding of males and females of the same age varies with the season: after spawning females feed much more intensively than males; in July and August males feed more intensively. Females consume more fish than males.

The assortment of food components, their sizes and quantity change with growth. Young of all populations feed on zooplankton. Fishes aged 2 years eat Mysidae, Amphipoda, Insecta larvae and fishes. The importance of fishes increases with age.

In winter the smelt feeds very little. As a rule smelt abstain from feeding during the spawning and pre-spawning period (Nikolsky, 1956, and others).

3.42 Food

Young and adults of small freshwater smelt feed on planktonic Crustacea: Cladocera (Bosmina sp., Daphnia sp. etc.) and Copepoda (Cyclops sp., Diaptomus sp. etc.). The main food groups of adults of different populations are Mysidacea, Amphipoda and young fish. The smelt of the Atlantic coasts of North America feeds on pelagic Isopoda (Kendall, 1927). The diet of the White Sea smelt consists of 60 components (Kudersky and Russanova, 1963), Polychaeta playing the main role (mainly Nereids which do not occur in smelt diet in other areas).

3.43 Growth rate

According to Belyanina (1968) all smelt populations may be divided into 2 groups based on character of the growth rate during ontogeny: (1) populations whose individuals grow most intensively during their first year of life; then the growth rate decreases comparatively sharply (smelt populations of West and East European basins, excluding the extreme North, and North-American waters); (2) populations whose individuals grow comparatively slowly during their first year while their rate of growth increases more or less sharply during their second year. Then it decreases gradually (smelt populations of the White Sea, the Cheshskaya Bay and Siberian coasts). Sizes of individuals of different smelt populations in successive years of life are given in Table VIII. Values of the linear growth (in % to maximal length) of some populations of both groups are shown in Fig. 14.

Condition factor (Ponderal index)

The well-known length-weight relation in fish may be expressed by the following equation:

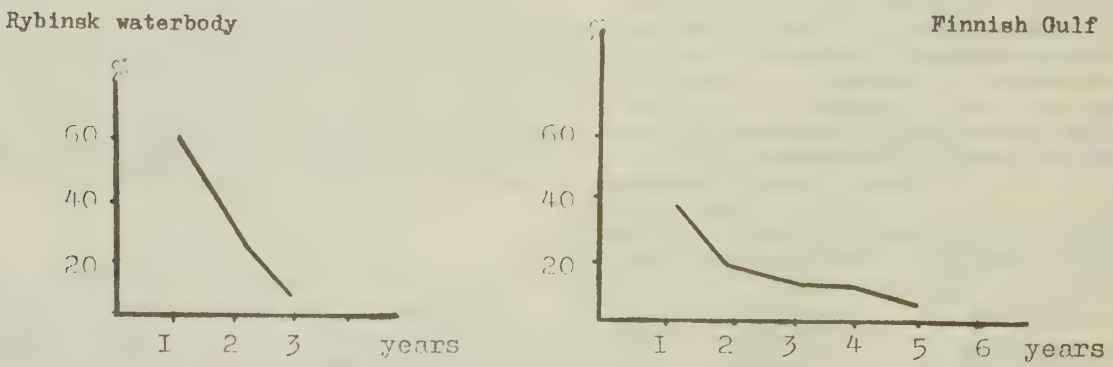
$Q = Al^n$, where Q = weight, l = length, A = const., n = near 3

Values of "n" for different smelt populations are given in Table XIX.

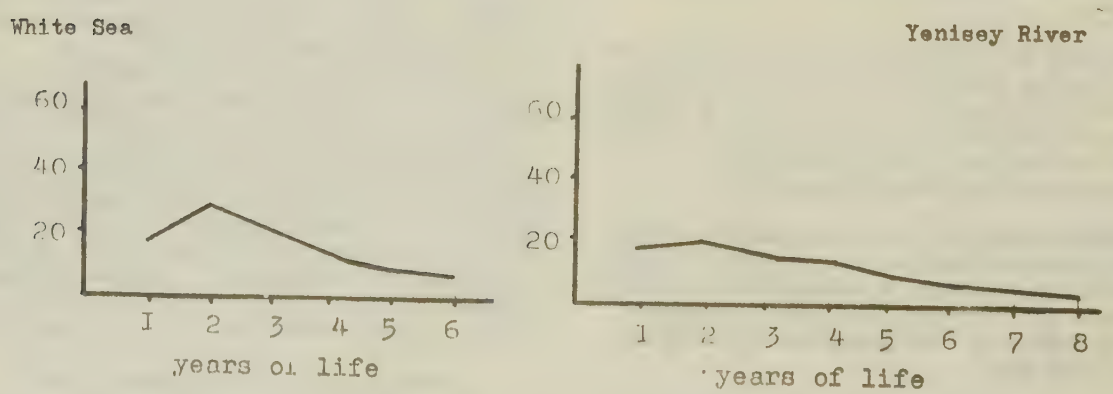
TABLE XIX

Values of "n" for different smelt populations

	Locality	n	Authority
Landlocked	White lake	2.70	Schetinina, 1954
	Rybinsk waterbody	2.91	Schetinina, 1954
	Kurishes Haff	2.87	Marre, 1931
	Great lakes	2.82	Lillelund, 1961
Sea-migrant	Elbe river	3.28	Lillelund, 1961
	Miramichi river	3.20	McKenzie, 1958; Lillelund, 1961
	White Sea:		
	Kandalaksha Bay	3.48	Original data
	Dvina Bay	3.36	Kirpichnikov, 1935
	Yenisey river	3.15	Tyurin, 1924 and others



A. Populations of the 1-group



B. Populations of the 2-group

Fig. 14 Linear growth of fish in successive years of life (as % of maximal length) of different smelt populations (from Belyanina, 1968).

TABLE XX

Rate of growth in different smelt populations
(from data in Table VIII)

Locality	Length increase in successive years of life											
	1	2	3	4	5	6	7	8	9	10	11	12
Freshwaters												
Pskov-lake	7.2	2.9	3.2									
Ilmen lake	5.2	3.0	2.5									
Valday lake	5.3	4.6	1.3									
White lake	6.0	2.5	2.5									
Rybinsk wtb	5.9	2.8	0.7									
Kurishes Haff	6.3	4.2										
Dadey lake	7.1	3.6	1.5	1.5								
Lazmiaden lake	8.2	1.1	2.5	1.1	2.9							
Ladoga lake	8.0	1.5	1.2	2.9	2.2	2.5						
Onega lake	6.3	2.5	0.6	1.2	0.4	0.3	0.5	0.5				
Michigan	9.2	6.5	1.4									
Upper lake	6.5	8.3	4.2	2.3	1.2	2.3	1.2					
Sea-migrant												
Elbe river	7.1	6.3	3.9	3.9	2.6							
Finnish Gulf	7.8	3.3	2.5	2.4	1.6							
White Sea:												
Onega Bay	4.7	5.4	4.4	4.7	4.0	4.2						
Dvina Bay	4.1	5.2	3.9	3.7	2.2	2.4	3.1	2.8	0.7			
Kandalaksha Bay	4.7	8.2	5.9	3.8	2.4	2.0						
Chesha Bay	3.5	4.6	4.4	2.7	2.5	2.8	1.7					
Yenisey river	4.5	5.3	4.3	3.5	2.7	2.0	1.6	0.5	1.1			
Lena river									3.8	2.9	1.2	1.3
Amur river	5.5	6.0	3.5									

The populations of the first group live under temperate climatic conditions. Their season of growth lasts 6-7 months. They live in waters with a good supply of small zooplankton which the fry and young feed on; the plankton biomass is about 300-1300 mg/m^3, as may be concluded from various literature sources. The rate of growth of freshwater landlocked populations decreases sharply during ontogeny (Belyanina, 1968; Tables VIII, IX, XIX, XX; Fig. 14). Populations of the second group live under severe sub-arctic conditions. Their season of growth lasts 5-6 months (White Sea smelt) or only 4 months (East Siberian populations). The average zooplankton biomass is about 50-300 mg/m^3 during the season. The later spawning period (May-June and even July) compared to that of the European and American populations (March-April), the lower temperature during the season, the earlier cold in autumn, the poorer food resources - all these factors determine the slow growth-rate of the young smelt of these regions. However, rate of growth increases during the second year of life and greatly exceeds that of the first year (Fig. 14). This is evidently a result of changes in feeding habits; the smelt begins to feed on larger Crustaceans (Amphipoda, Mysidacea). The Kandalaksha Bay smelt (White Sea) is remarkable for its most rapid growth (linear and weight) during the second (and third) year of life (Tables VIII, IX, XIX). This population lives under conditions of higher salinity (25-28 °/oo) than do all other smelt populations. The food resources of the White Sea are richer than those of estuaries of Siberian rivers; the average biomass of benthos of the White Sea is about 10-30 g/m^2 (excluding Mollusca and Echinodermata which smelt does not feed on), while this value is only 4-5 g/m^2 for the estuaries of the Siberian rivers (Grese, 1957, and others). Also the Kandalaksha Bay smelt feeds intensively on heteronereid stages of Polychaeta, mainly Nereis virens (Abdel-Malek), 1963; Kudersky and Russanova, 1963), which is an easily accessible and very abundant food in this region.

The length of the growth season is different for different age groups: young fish begin to grow earlier and finish the season later than older individuals (Lillelund, 1961 and others). This may be related to spawning in spring or in the beginning of summer.

Smelt grow faster in warm years and slower in cold ones (Kirpichnikov, 1935; Meshkov and Sorokin, 1952, original data on the White Sea smelt). The effect of temperature on growth is seen more clearly in younger fish.

Generally strong year-classes grow more slowly than weak ones (Lillelund, 1961; Morosova, 1960, and original data). According to Abrosov and Agapov (1957) the rate of growth of the small smelt of the Jijitzkoye lake decreases with increasing population density.

3.44 Metabolism

The metabolism of smelt has not been studied.

Leviyeva (1952), Kleimenov (1962) and some others give data on the chemical composition of smelt (Table XXI). Data on fat are shown in Table XXII. Siberian smelt have the most fat in the body and reproductive products. The small smelt of the Upper Volga system have the lowest fat content. During the spawning period the fat content of the body and internal organs of males (except gonads) is higher than that of females. Chechenkin (1952) reported that the fat of the Pskov lake smelt consists mainly of non-saturated fatty acids, with oleic acid dominant.

Fatness changes during life and by seasons (Belyanina, 1966b). Localization of fat in smelt (in per cent to total fat) is shown in Table XXIII.

Ripening of the female gonads results in considerable changes in the localization of fat and its breakdown. The fat of the intestine and mesenteries is used up almost entirely. This process is much less intensive in males. According to Belyanina and Makarova (1965) a female smelt uses up about 65% of initial fat during spawning, 53% being removed as fat of extruded eggs and 12% being used in activity. A male uses up about 47% of its fat, fat in extruded reproductive products being 6–10%; a great part of the fat is used in activity during spawning.

Endocrine systems and hormones and osmotic relations of the smelt have not been studied.

3.5 Behaviour

3.51 Migrations and local movements

During most of the year smelt stay near shores. After spawning the fish migrate to deeper water, evidently to avoid high temperatures. In autumn fish of all age-groups keep together. Smelt tend to form local populations. Feeding migrations of smelt are short. They spend the winter at river mouths. In spring they migrate to spawning areas upstream. Extent of spawning migrations is given in Table XXIV, season of migration in Table XV. After spawning adult smelt actively move downriver, prolarvae drift passively.

Differences in the migratory behaviour of different populations are mentioned in Section 3.12.

3.52 Schooling

Evidently smelt form schools during all stages of the life cycle (Kendall, 1927 and others). By our observations only the largest and oldest examples of White Sea smelt (6–8 yr old) do not form schools but search for fish alone. Spawning and wintering concentrations are rather dense, and feeding schools are of less density. In autumn and winter, smelt concentrations consist of fish of both sexes and different age groups. In spring, mature individuals form spawning schools, grouping by size or age.

Gobiids, flatfishes and other species sometimes occur in fishing nets together with the White Sea smelt; herring, stickleback, sprat and others with the Finnish Gulf smelt.

Larvae and young smelt feeding on plankton perform vertical movements (Amstislavsky, 1963; McKenzie, 1964).

The behaviour of spawning schools is discussed in Section 3.16.

3.53 Responses to stimuli

Kendall (1927), Baldwin (1948), Dryagin (1948) and others have noted that adult smelt avoid strong light. Strong light destroys developing eggs. Hatching larvae react positively to light (Unanyan and Soin, 1963).

Unanyan and Soin (1963) noted that seawater of 26 ‰ salinity has a harmful effect on the reproductive products of smelt, preventing fertilization. Seawater of salinity above

TABLE XXI

Chemical composition of smelt
(from Leviyeva, 1952 and Kleimenov, 1962)

Organ	Month	Chemical composition (%)							Calorific value
		Water	Fat	Total N	Protein N	Extractive N	Total protein (=N 6.25)	Ash	
Neva river:									
males	May	75.4	5.2	2.67	1.97	0.70	16.69	2.56	
(entire)	June	79.5	3.3	2.39	1.96	0.43	14.94	2.30	85.2-89.7
Females	May	76.4	3.9	2.77	2.13	0.64	17.31	2.52	
(entire)	June	81.4	2.1	2.27	1.84	0.43	14.19	2.31	
bodies	June	81.4	1.4	2.49	1.94	0.55	15.56	1.84	
heads	May	78.4	2.9	2.20	1.43	0.77	13.75	4.45	
	June	80.6	2.9	2.05	1.48	0.57	12.81	4.41	
livers	May	74.9	7.6						
	June	79.8	3.9						
internal organs without reproductive products	May	59.7	27.3						
	June	78.3	8.3						
Far East									
entire	May	77-78	4.4-5.0				16.1-17.0	1.0-1.1	110.6
eggs		62	12.0				23.0	2.0	
testis		66	7.0				24.0	3.0	

Contents in mg/100g

K	Ca	Fe	Mg	P	$(CH_3)_3NO_3$
388	83	0.7	20	246	335

Aminoacid content as % of protein

Isoleucine	Leucine	Lysine	Methionine	Phenilalanine	Treonine	Valine
4.8	7.8	11.1	2.8	4.0	4.3	5.4

There are 2340 international units of vitamin D in 1 g of smelt liver fat and 170-200 i.u. in 1 g of fat of internal organs

TABLE XXII

Fat content of spawning smelt from different populations

Locality	Fat content in % of wet substance			Authority
	body	eggs	testis	
White Sea	1.7 - 3.9	8 - 9	5	Belyanina, 1966b
Neva river	2.5 - 3.5	-	-	Leviyeva, 1952
Siberia	4.7 - 5.3	12	7	Kyzevetter, 1949
Uchinskoye waterbody	0.5 - 2.4	4.8 - 7.7	6	Original data
North Germany	-	10.2	5.1	Morawa, 1956

TABLE XXIII

Localization of fat in smelt (as % of total fat)

Locality	Sex	Organ	Season		
			April-May	August	October
White Sea	Females	body	44-53	59-65	72
		gonads	45-57	2-3	7
		other internal organs	to 4	33-38	21
	Males	body	78-88	63-79	
		gonads	6-12	4-6	
		other internal organs	to 16	20-33	
Uchinskoye waterbody and Rybinsk waterbody	Females	body	36	77	
		gonads	64	8	
		other internal organs	very little	15	
	Males	body	61	78	
		gonads	7	7	
		other internal organs	32	15	

TABLE XXIV

Extent of upriver migrations in different smelt populations

Locality	Extent of migration (km)	Authority
Yenisey river	1000	Tyurin, 1924, and others
Lena river	180-200	Pirojnikov, 1950
Amur river	270	Kuznetzova, 1962
Suyfun river and other rivers of the Far East	16-18	Ivanova, 1955
Elbe river	120	Lillelund, 1961
Rivers of the White Sea basin	2-3	Balagurova, 1957 and others
Saint Lawrence river	300	Magnin and Bealieu, 1965
Miramichi river	50	McKenzie, 1964

13 $^{o}/_{oo}$ results in pathological changes in developing eggs: flowing out of yolk, deformation of body of embryo, absence of crystalline lens in eyes, destruction of brain, delay in hatching, sometimes death of embryos. Earlier stages of development (till complete gastrulation) are more sensitive to salinity than those later (after the embryo body has formed). Hatching prolarvae react positively to salinity by migrating downstream. Freshwater has a bad effect on the survival of smelt larvae in later stages of development (Unanyan and Soin, 1963). Lillelund (1961) stated that salinities below 10 $^{o}/_{oo}$ have no harmful effect on developing eggs and larvae. The upper limits of thermal tolerance during early stages of development of eggs lie within the range 17.7-20.7°C, at later stages within the range 21-24°C.

4 POPULATION

4.1 Structure

4.11 Sex ratio

According to Kirpichnikov (1935) males predominate in the majority of smelt populations. The number of males decreases in older age-groups because of their shorter life cycle (Table XXV). A decrease in the relative number of males in each age-group may be seen on comparing the sex composition of spawning and feeding concentrations. This may be caused by the higher total mortality rate of males during spawning (Tremblay, 1946).

The sex ratio on spawning grounds is discussed in Section 3.16.

4.12 Age composition

The age composition of different spawning populations is given in Table XXVI. Catches of feeding and wintering concentrations include some younger immature fishes.

For age at first capture, age at maturity and maximum age see Table VIII. Most of the spawning (and fishing) stocks are formed by fish of minimal spawning age - See Table XXVI.

4.13 Size composition

Data relating length to age and maturity in different stocks are given in Table VIII.

The length-weight relationship of different stocks is given in Table XIX.

4.2 Abundance and density (of population)

4.21 Average abundance

According to McKenzie (1964) the smelt stock of the Miramichi river is estimated about 375 million fish; Lillelund (1961) estimated the stock of the Elbe river of 60-85 million fish.

4.22 Changes in abundance

Domrachev and Pravdin (1926), Petrov (1940, 1947), Dryagin (1948) and others have noted sharp changes in abundance in short-lived smelt populations. Lapin (1960) gave an analysis of causes of that phenomenon. Sharp decreases in abundance are related to poor density of one or two year classes. Usually the population density recovers in several years. Sometimes a fall in density is a result of an epidemic (Van Oosten, 1947; Patterson, 1948, and others). In most areas fishing has no

TABLE XXV

Sex ratio in different age-groups of White Sea smelt (original data)

Year and season of sampling	Sex	Age groups 2	3	4	5	6	7-8	Number of fishes
1961								
Spawning concentrations (spring)	Females	-	41.5	37.0	100	100	100	184
	Males	-	58.5	63.0	-	-	-	270
Feeding concentrations (summer)	Females	52.1	54.5	75.0	75.0	100	100	234
	Males	47.9	45.5	25.0	25.0	-	-	192
1962								
Spawning concentrations (spring)	Females	-	66.0	50.0	72.7	66.7	100	335
	Males	-	34.0	50.0	27.3	33.3	-	282
Feeding concentrations (summer)	Females	52.1	56.7	70.5	100	-	-	152
	Males	47.9	43.3	29.5	-	-	-	127

TABLE XXVI

Age composition (%) of spawning stocks in different smelt populations

Locality	Age groups															Authority
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Pskovsko-Chudskoye lake	90	10														Meshkov & Sorokin, 1952
Rybinsk waterbody	17	77	6													Sobetinina, 1954
Dadey lake	74	17	8	1												Willer, 1926
Lazmiaden lake	6	37	38	15	4											Willer, 1926
Ladoga lake	6	24	32	25	11	2										Arkhiptzeva, 1956 and others
Onega lake		4	28	40	20	7	1									Alexandrova, 1963
Miramichi river		66	30	4												McKenzie, 1964
Huron lake		54	38	8												Baldwin, 1948
Upper lake		32	49	17	1	1										Bayley, 1964
Neva river		1	28	42	24	3	1	1								Kojevnikov, 1949
White Sea:																
Onega Bay		7	32	41	17	3										Balagurova, 1957
Kandalaksha Bay			30	46	23	1										Original data
Yenisey river					8	20	43	23	6							Kravchuk, 1958
Lena river							6	14	8	39	28	5				Pirojnikov, 1950
Chatanga river								3	10	10	19	28	25	4	1	Lukyanchikov, 1964
Anadyr river				17	21	33	13	7	4	3	1	1				Agapov, 1941

serious effect on population density, but Morosova (1960) and Amstislavsky (1963) have stated that intensification of the fishery has led to a sharp decrease of catches in the White lake (Vologda district) and the Ob estuary.

4.24 Changes in density

Annual variations in landings per unit of fishing effort for the Miramichi river, Canada, are given in Fig. 17.

Smelt occur in relatively shallow waters.

Seasonal variations in the available stock are mentioned briefly in Section 3.52

4.3 Natality and recruitment

4.31 Reproduction rates

Rupp (1959) found that the survival rate of eggs of the smelt of Maine is about 6%. According to Kojevnikov (1949) survival coefficient (from eggs to adult) in the Neva river smelt is about 0.02%.

4.32 Factors affecting reproduction

See Sections 3.16, 3.21, 3.22, 3.23

4.33 Recruitment

Slowly growing year classes mature and join fishable stocks later than those which grow faster. Unpublished data show that the 1958 year-class of White Sea smelt grew slowly during the first year of life and reached maturity only at the fourth year (only 20% matured at the third year of life). The 1959 and 1960 year classes grew faster and matured during the third year of life. Similar data are given by Morosova (1960) and Lillelund (1961).

Recruits enter the spawning stock in spring. The relative number varies from year to year because of differences in the strength of year-classes and in the rate of maturing (see above and 4.22).

4.4 Mortality and morbidity

4.41 Mortality rates

According to Lillelund (1961) average fishing mortality coefficient in the Elbe river smelt is 0.17; natural mortality coefficient for different age groups is as follows:

Age	1	2	3	4
Mortality coefficient	0.90	1.08	1.30	1.59

McKenzie (1964) stated that average annual fishing mortality coefficient in the Miramichi river smelt is about 3-5% of the stock.

4.42 Factors causing or affecting mortality

Predators: See Sections 3.15, 3.22, 3.34.

Food of larvae and post-larvae and its availability: See Section 3.22.

Physical factors: See Sections 3.15, 3.17. Sometimes stocks of smelt become frozen in ice during the spawning migration in Siberian rivers.

Direct effects of fishing: See Section 4.41.

Indirect effect of fishing:

Samsonov (1910) showed that great mortality of eggs of freshwater smelt is caused by fishing gear.

4.43 Factors affecting morbidity

Parasites and diseases: See Table XVII

It is well known (Van Oosten, 1947, and others) that mass morbidity and mortality of smelt occurred in the Great Lakes in 1942/43. The epidemic was apparently caused by a virus or a bacterium.

Physical factors causing morbidity of adult smelt are not known.

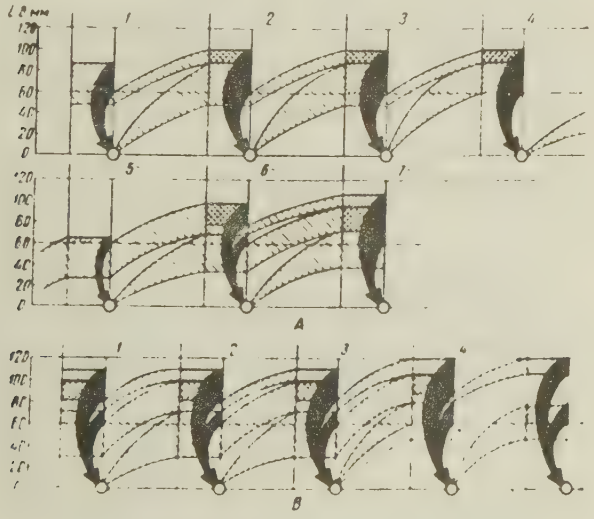
4.5 Dynamics of populations (as a whole)

Lillelund (1961) gave a model of dynamics of year-classes in the smelt population of the Elbe river in 1953-60. Lapin (1960) has worked out a scheme of dynamics of age-groups in the population of the small smelt of the Rybinsk waterbody (Fig. 15). This model is made on the assumption that the Rybinsk smelt spawns once only before death. The model demonstrates that different rates of growth and maturing may cause changes in the age composition of the stock.

4.6 The population in the community and the ecosystem

Pirojnikov (1955) included the Siberian smelt in the Arctic freshwater complex of fish (Hucho hucho, Salvelinus fontinalis, Stenodus leucichthys, Coregonids). Ponomareva (1949) noted that smelt larvae in the Kara estuary occur together with larvae of Coregonus autumnalis, Salvelinus fontinalis, Myoxocephalus scorpius, Liopsetta glacialis and Eleginus navaga.

See also Sections 3.33, 3.34, 3.42



- mature fish of one-year old
- mature fish of two-year old
- mature fish of three-year old
- immature fish

Fig. 15 Scheme of dynamics of year-classes in populations of small smelt (from Lapin, 1960). Seasons are shown on the horizontal axis, body length on the vertical. Arrows show that an age-group (or part of it) has reached maturity and spawned in spring (circles signify laid eggs). The dotted line on the level of 60 mm shows that smaller fishes remain immature. Two cases (A and B) with different initial age structure of population are considered.

5 EXPLOITATION

5.1 Fishing equipment

5.11 Gears

In the Elbe river they catch smelt in river-stow-nets, which lie on either side of a cutter, or the nets may be anchored to the bottom of the river. Each cutter has one or two river-stow-nets (Lillelund, 1961). In the Great Lakes they use nylon gill nets of 25-38 mm mesh or smaller (extension measure); these are 75 m long. Otter trawls are used also; these are semiballoon type, with head-rope lengths of 945-1250 cm and mesh sizes of 62 mm in the wings and body and 12 mm in the cod end. Shore seines are used during the spawning run; these are of 12 mm-mesh cotton twine, 180 cm deep and 76 m long. Smelt from rivers are captured at sea-lamprey barriers in weir traps of 120 x 180 x 180 cm, constructed of 6 mm-mesh (bar measurement) hardware cloth over wooden frames. Spawning run smelt are captured in commercial pound nets 210 cm deep made of cotton twine of 30 mm mesh, shrunk to about 24 mm mesh through treatment with preservatives. The boom shocker consists of two electrical wire paddles suspended from booms extending ahead of a 16-ft outboard-powered boat. Power for the shocker is supplied from a portable 2.5-kw, 220-volt, 3-phase, AC generator (Bayley, 1964).

According to McKenzie (1964), in the Miramichi River "open-water fishing gear is used at the beginning of the season unless the ice is strong enough to set winter fishing gear. Open-water gear consists mostly of bag nets set on stubs or pickets near shores protected from the full force of storms. The gear is fished from catamarans and man-propelled scows 6-9 m long".

In Russia, smelt is fished by special traps ("mereja") made of small-mesh cotton twine stretched on 4-6 hoops of wood with two wings. Traps are fixed by anchors at mouths of spawning rivers. Shore seines of 80-170 m long with mesh sizes of 32-30-28-26-20-18-16 mm in wings and 16-12-8 mm (inwards) in the cod end (Tyurin, 1939). Large river-fixed-nets and trawls are used also.

Angling for smelt occurs also in some regions (Canada, north-western part of USSR). Baits are earth worms and young fishes.

During the development of the fishery there has been a tendency to change from simple traps and cotton gill nets to nylon gill nets, trawling and electrical fishing.

Echosounders and fish detectors are not used by smelt fishermen.

Smelt is frightened by light, and effective methods of attracting the fish are not known.

5.12 Boats

In Europe smelt are usually fished from motor boats of 12-14 m long and 4.5 m wide of 40-75 hp (Lillelund, 1961). In North America catamarans and man-propelled scows of 6-9 m long are frequently used (McKenzie, 1964).

5.2 Fishing areas

5.21 General geographic distribution

Within the area of distribution (see Fig. 9) smelt are fished in coastal waters of seas, estuaries of rivers and lakes. During the spawning period smelt are fished in rivers.

5.22 Geographic ranges

See Section 5.21

Smelt are most abundant in the north-western part of U.S.S.R. and the Amur river basin, Atlantic coasts of Canada and U.S.A.

New ranges of smelt fishery are: Great lakes, where the smelt was introduced in the first quarter of the twentieth century (Speirs, 1951); estuaries of Siberian rivers, where the smelt fishery did not develop until after 1935; artificial waterbodies of the Upper and Middle Volga system.

5.23 Depth ranges

Smelt occur in midwater or near the bottom in relatively shallow places. The young stages carry out vertical migrations in pursuit of plankton.

5.3 Fishing seasons

5.31 General pattern of season(s)

Smelt are caught mainly in spring, during spawning. The fishing season is rather short (see Sections 3.16, 5.33). In autumn the fishery is based on less dense concentrations than in spring. In winter angling is used (McKenzie, 1964, and others).

5.32 Dates of beginning, peak and end of season(s)

The beginning of the fishing season coincides with the formation of offshore feeding concentrations in autumn and continues in winter. The peak of the fishing season is based on spawning concentrations (see Table XV). The season ends after spawning when smelt have migrated to deeper waters.

5.33 Variation in date or duration of season

The fishery for spawning smelt is influenced by water temperature and other factors which control spawning (see Section 3.16).

According to McKenzie (1964) the fishing season in the Miramichi river basin from 1931-1963 varied irregularly from 77 to 136 days. This variation in length of season appears to have little effect on the final total catch.

The highest proportion of large smelt is caught early in the spawning season. Size of fish declines as the season progresses, and the price of fish decreases.

5.4 Fishing operations and results

5.41 Effort and intensity

Lillelund (1961) and McKenzie (1964) have given statistics of the smelt fishery in the Elbe river and the Miramichi river for many years, including data on catches per unit of fishing effort. Data on Miramichi annual commercial smelt landings, 1931/32-1962/63, and catch per licensed net per season are given in Figs. 16, 17.

5.42 Selectivity

Bayley (1964) reported that "the gill nets from 25-125 mm mesh captured almost exclusively fish of age group II or older. The shore seine, weir trap and pound-nets, fished only in the spring, sampled solely the spawning population. Since segregation by maturity precedes the spawning migrations, immature specimens (all fish of age-group I and part of age-group II) were absent. The otter trawls and boom shocker fished at times other than the spawning period, appeared to be the least selective gears. Trawl collections usually included smelt of all sizes and age groups. The boom shocker fished only in shallow water seemed to sample adequately in the waters fished".

According to McKenzie (1964) "Increasing the mesh size from 29-32 mm increased the gilling 5 times and in the 38 mm net 7 times. Most smelt under 10 cm escape the commercial nets. Size selection by the nets is one of the factors causing diminution in the size of smelt caught as the commercial season progresses".

5.43 Catches

Total annual yields for various countries are given in Table XXVII and average yields for different fishing grounds in Table XXVIII.

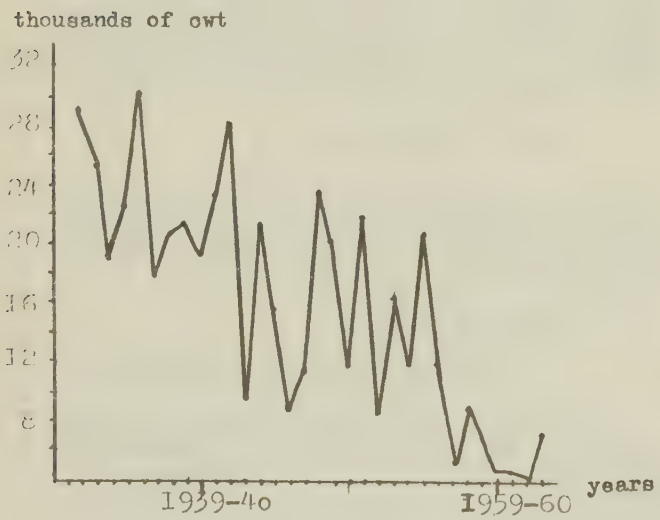


Fig. 16 Miramichi annual commercial smelt landings, 1931-32 to 1962-63. (from McKenzie, 1964).

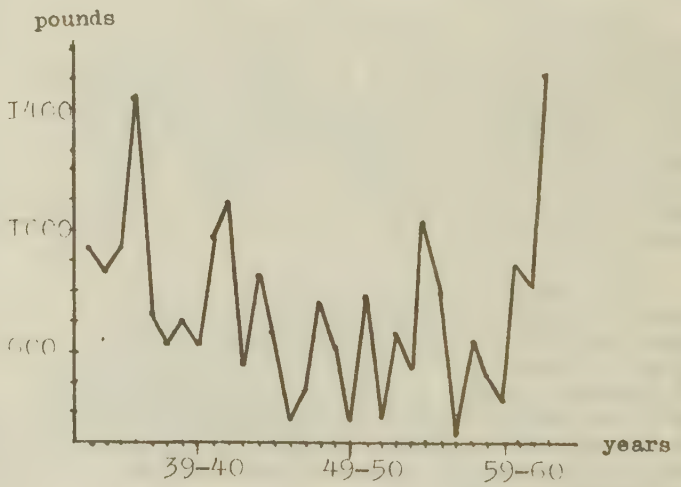


Fig. 17 Miramichi smelt catch per licensed net per season (from McKenzie, 1964).

TABLE XXVII

Total annual yields of smelt in various countries
(thousands of metric tons)
(Yearbook of Fishery Statistics FAO, 1966)

Country	Years						
	1958	1961	1962	1963	1964	1965	1966
Total	25.0	27.0	25.0	25.0	29.0	28.0	28.0
U.S.S.R.	14.5	15.1	15.3	15.5	16.1	16.7	16.6
Canada	4.3	7.3	1.5	1.6	2.1	2.1	2.1
U.S.A.	6.0	2.5	2.2	2.3	2.4	1.8	1.4
Finland	0.1	1.1	0.6	0.4	0.7	0.8	0.9
France	-	0.3	0.2	0.1	0.1	-	-
Federal Republic of Germany	0.4	0.2	0.2	0.2	0.4	0.3	0.3
Netherlands	0.2	0.1	0.2	0.1	0.2	0.3	0.3
Norway	-	0.9	-	0.1	0.6	0.2	0.2

TABLE XXVIII

Average annual yields from different fishing grounds

Fishing grounds	Average yield (tons)	Years	Authority
Pskovsko-Chudskoye lake	3600	1931-1963	Shirkova & Pihu, 1966
Ilmen lake	363	1946-1958	After Kudersky, 1962
White lake	261	1945-1958	After Kudersky, 1962
Onega lake	623	1945-1959	After Kudersky, 1962
Ladoga lake	1374	1946-1954	After Kudersky, 1962
Neva river	400	1932-1948	After Kojevnikov, 1949
Finnish Gulf	640	1932-1948	After Kojevnikov, 1949
Kurishes Haff	983	1948-1957	After Noskov, 1959
Elbe, Eider, Weser	311.5	1955-1959	Lillelund, 1961
White Sea	400		
Yenisey	150.7	1946-1955	Podlesnyy, 1958
Ob estuary	max.1540	1960	Amstislavsky, 1963
Amur	1000	1949-1958	Kuznetzova, 1962
Miramichi river	726	1931-1963	McKenzie, 1964
Great lakes	7264	1960	Bayley, 1964

6 PROTECTION AND MANAGEMENT

6.1 Regulatory (legislative) measures

6.11 Limitation or reduction of total catch

In many cases catches of smelt may be increased, as only a small part of the population is removed by fishing. However, in some cases it is necessary to limit catches (Morosova, 1960; Amstislavsky, 1963).

6.12 Protection of portions of population

The size of caught smelt is limited by the market: for example in the Elbe river they do not catch smelt smaller than 14 cm (Lillelund, 1961).

6.2 Control or alteration of physical features of the environment

Physical features of the environment may be altered to improve spawning grounds by clearing such impassible obstacles as brush jams, old dams, steep rapids or falls, sluiceways, pulpwood, logs as well as road culverts. McKenzie (1964) noted that "at moderate cost much can be done to overcome these situations. Streams full of brush and debris from lumbering operations can be cleared and laws enforced to prevent recurrences. Old dams can be removed or if in use can in some cases be opened during the smelt spawning season. "Smeltways" can be built also to permit passage over the dams. Grades through culverts should be made to conform to the slope of the original stream bed with addition of baffles, if necessary, to break the swift smooth flow. The bottom of the culvert at the outfall (at least when built) should be level with, or preferably lower than the stream bed. Action to facilitate the passage of smelt through highway culverts to their spawning grounds would be of considerable importance to the smelt fishery in New Brunswick. Smelt often escape the strong currents in streams during spring freshets by going out over banks and spawning far from the regular stream bed. In some locations it seems practical to prevent loss of both eggs and parents from stranding by constructing dykes. In the larger Miramichi branches and tributaries flood control by means of dams would no doubt increase the larval production".

6.5 Artificial stocking

6.52 Transplantation, introduction

Transplantation of smelt from the Green lake (Maine) into the Crystall lake (Michigan) was made in 1912 and in following years and has given excellent results (Van Oosten, 1937; Creaser, 1926, 1929, and others). Smelt has spread all over the Great lakes and formed a good fishery population there (Table XXVIII). In Russia smelt was repeatedly transplanted into some lakes of the Leningrad and Novgorod Districts (Tikhiy, 1941). These operations have given good results in 42% of cases for small smelt but for long-lived smelt only 17% have been successful. As a rule unrepeated transplantation has rarely given good results. Smelt was introduced into some Ural lakes also (Karabak, 1930). Some introduction of smelt into the waters of Karelia were proposed by Stefanovskaya (1957).

7 POND FISH CULTURE

7.9 Transport

Smelt has not been cultured in ponds. According to Karabak (1930) and Suvorov (1939) smelt eggs may be incubated and transported in a cool wet atmosphere. Mortality of eggs during 5-6 days is less than 5% (Karabak, 1930). Good survival of transported smelt eggs and larvae was noted by Richardson and Belknap (1934), fishes of 6-10 cm length being the most hardy. Early larvae are too delicate and they should not be transported. Smelt eggs are gathered on special screens during the spawning period.

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SYNOPSIS OF FISHERIES BIOLOGICAL DATA

This is one of a series of documents issued by FAO, CSIRO and USFWS concerning species and stocks of aquatic organisms of present or potential economic interest. The primary purpose of this series is to make existing information readily available to fishery scientists according to a standard pattern, and by so doing also to draw attention to gaps in knowledge. It is hoped that synopses in this series will be useful to other scientists initiating investigations of the species concerned or of related ones, as a means of exchange of knowledge among those already working on the species, and as the basis for comparative study of fisheries resources. They will be brought up to date from time to time as further information becomes available either as revisions of the entire document or their specific chapters.

The relevant series of documents are:

RAO	Fisheries Synopsis No. replacing, as from 1.1.63 FAO Fisheries Biology Synopsis No.	FR/S FB/S
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